INFLUENCE DU PAYSAGE SUR UNE COMMUNAUTÉ DE STRIGIDÉS EN TENANT COMPTE DE LA PROBABILITÉ DE DÉTECTION

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Mémoire présenté au Département de biologie en vue
de l'obtention du grade de maître ès Sciences (MSc.)

FACULTÉ DES SCIENCES

UNIVERSITÉ DE SHERBROOKE

Sherbrooke, Québec, Canada, janvier 2010

Your file Votre référence
ISBN: 978-0-494-61466-2
Our file Notre référence
ISBN: 978-0-494-61466-2

Le 15 janvier 2010

le jury a accepté le mémoire de Madame Geneviève Perreault dans sa version finale.

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Plusieurs études ont tenté de décrire l'influence de la structure du paysage sur la distribution des Strigidés. Certaines ont même essayé de quantifier l'impact de la perte et de la fragmentation d'habitas sur ces oiseaux. Cependant, la majorité de ces études n'ont pas tenu compte de la probabilité de détection imparfaite lors de l'échantillonnage, ni considéré que les interactions entre les différentes espèces pouvaient interférer avec cette distribution. Dans cette étude, je mesure l'influence de la structure du paysage sur la distribution du Grand-duc d'Amérique (*Bubo virginianus*), de la Chouette rayée (*Strix varia*) et de la Petite Nyctale (*Aegolius acadicus*) parmi 112 sites répartis à travers un large gradient « forêt-agriculture » dans le Sud du Québec. Je mesure également l'impact des interactions interspécifiques sur cette distribution. Afin de déterminer si la séquence d'enregistrements utilisée lors des recensements de Strigidés affecte la détection de ceux-ci, je compare les probabilités de détections obtenues dans les recensements où le chant d'une seule espèce est diffusé avec celles des recensements où le chant d'une espèce est diffusé suite à celui d'un compétiteur ou d'un prédateur. Finalement, j'effectue deux versions des analyses afin de comparer les résultats obtenus à l'aide de simples régressions logistiques à ceux obtenus lorsque la probabilité de détection est considérée. Mes résultats indiquent que la probabilité d'occurrence du Grand-duc d'Amérique ne semble pas être affectée par la composition du paysage et que sa probabilité de détection n'est pas influencée par la séquence d'enregistrements utilisée lors de l'inventaire. Par ailleurs, la probabilité d'occurrence de la Chouette rayée et de la Petite Nyctale augmente avec le couvert forestier et, par le fait même, diminue avec le couvert agricole. La présence d'un prédateur ou d'un compétiteur dans le paysage ne semble pas influencer la distribution des Strigidés. Cependant, les chants du Grand-duc d'Amérique diminuent la détectabilité de la Chouette rayée. Bien que les chants du Grand-duc ne semblent pas affecter la détectabilité de la Petite Nyctale en tant que telle, la probabilité de détection de celle-ci est toutefois moins élevée lorsque le chant du Grand-duc d'Amérique est diffusé avant son propre chant. Finalement, j'obtiens des résultats différents en considérant la probabilité de détection ou non. Plus précisément, certaines variables avaient un effet significatif dans une seule version des analyses, ou encore la magnitude de l'effet était différente selon le type d'analyse utilisé. Ceci laisse sous entendre que plusieurs paramètres peuvent influencer la probabilité de détection des Strigidés et qu'elle devrait toujours être considérée dans les recensements de rapaces nocturnes.

REMERCIEMENTS

Je tiens à remercier mon directeur de recherche, Marc Bélisle, qui a accepté de superviser ce projet qui débordait de ses champs d'études habituels. La liberté qu'il m'a offerte dans la réalisation de ce projet a été pour moi une grande source de motivation. Ses connaissances en statistiques ont également été une véritable mine d'or pour une étudiante qui partait de loin dans ce domaine. « Entre toi, pis moi, pis la boîte à pain », un gros merci!

Je remercie également mes deux compagnons de route, Benoit Gendreau et Marie-Claude Martin, qui ont accepté d'affronter la solitude, l'hiver et la nuit pour effectuer avec moi les 2240 recensements de rapaces nocturnes nécessaires à cette étude. Sans vous, je n'y serais jamais arrivée.

Merci à Dany Garant et Marco Festa-Bianchet d'avoir partagé leur point de vue sur ce projet. Merci à Marc Mazerolle pour son aide avec le logiciel PRESENCE, et à Caroline Girard et Gabriel Diab pour leur expertise en géomatique. Merci à Benoit Lapointe pour son aide dans les préparatifs du terrain et son incomparable disponibilité.

Finalement, merci à tous les membres du labo avec qui j'ai partagé un bout de chemin : Arnaud, Audrey, Claudie, François, Louis, Ludovic, Marie-Claude, Stéphane et Yanick. Merci pour le support moral, les encouragements, les échanges de services et les moments d'angoisses existentielles. Cette maîtrise n'aurait pas été aussi agréable sans vous!

Ce projet a été réalisé grâce au support financier de la Chaire de recherche du Canada en écologie spatiale et en écologie du paysage, la Fondation canadienne pour l'innovation, les Fonds québécois de la recherche sur la nature et les technologies, le Conseil de recherches en sciences naturelles et en génie du Canada, et l'Université de Sherbrooke.

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INTRODUCTION GÉNÉRALE

La foresterie, l'agriculture et l'urbanisation sont considérées comme les principales responsables de la perte et de la fragmentation des habitats naturels qui ont mené au déclin de nombreuses populations animales (Lehtinen et al.,1999; Carlson, 2000; Schmiegelow et Mönkkönen, 2002; Tscharntke et al., 2005). De plus, l'intensification des pratiques forestières et agricoles ont favorisé une homogénéisation du paysage qui exacerbe les problèmes causés par la perte et la fragmentation des habitats (Imbeau et al., 2001; Bélanger et Grenier, 2002; McCracken et Tallowin, 2004; Tscharntke et al., 2005). En plus de transformer la composition et la configuration du paysage, la perte et la fragmentation des habitats modifient la distribution et l'abondance des ressources disponibles (Redpath, 1995; Fahrig, 2003). Or, chaque espèce s'adapte différemment à ces changements, certaines ayant plus de facilité que d'autres (Deutschman et al., 1993; McKinney et Lockwood, 1999; Devictor et al., 2008). À titre d'exemple, en plus d'être influencés par les caractéristiques du paysage, la distribution des Strigidés peut être influencée par leurs interactions avec d'autres rapaces nocturnes (Hakkarainen et Korpimäki, 1996; Vrezec et Tome, 2004a, b). Pourtant, la majorité des études sur les Strigidés font abstraction de ces interactions. De plus, les interactions interspécifiques pourraient influencer la détectabilité des Strigidés lors des recensements et causer des biais lors de l'estimation de paramètres (Kelly et al., 2003; Olson et al., 2005; Crozier et al., 2006). Cependant, les programmes chargés de faire le suivi des rapaces nocturnes ne tiennent pas compte des ces interactions et ne sont pas corrigés pour une probabilité de détection imparfaite. Ce mémoire portera sur la probabilité d'occurrence et de détection de trois espèces de Strigidés au Québec, tout en considérant l'impact possible des interactions interspécifiques.

La perte et la fragmentation des habitats

Les effets de la perte et de la fragmentation des habitats sur les populations animales ont fait l'objet d'une pléthore d'études depuis 1970 (e.g., Andrén, 1994; Bender et al., 1998; Fahrig, 2003). Par exemple, il a été démontré que la plupart des espèces ont besoin d'une quantité

minimale d'habitat dans le paysage afin de pouvoir survivre (Andrén, 1994; Fahrig, 2003). C'est le cas, entre autres, du Pic à dos blanc (*Dendrocopos leucotos*) qui requiert au moins 9-17% de forêt décidue mature dans le paysage pour maintenir une population viable (Carlson, 2000). Par ailleurs, Bélisle et al. (2001) ont démontré que les habitats fragmentés contraignent les mouvements d'oiseaux forestiers comme la Paruline bleue (*Dendroica caerulescens*), la Paruline couronnée (*Seiurus aurocapilla*) et la Mésange à tête noire (*Poecile atricapillus*). Finalement, Hinsley (2000) a montré que la fragmentation augmente les coûts de déplacement de la Mésange charbonnière (*Parus major*).

Parmi les nombreuses études effectuées sur la perte et la fragmentation d'habitat, la terminologie n'a pas toujours été respectée et ces deux termes ont été utilisés à toutes les sauces. Comme son nom l'indique, la perte d'habitat est caractérisée par une diminution de la quantité d'habitat de bonne qualité dans le paysage. La perte d'habitat associée à une espèce donnée a donc toujours un impact négatif sur cette dernière (Fahrig, 2003). Pour sa part, la fragmentation a souvent été associée, à tort, à une certaine perte d'habitat. Pourtant, la fragmentation n'est que la division d'une ou de plusieurs parcelles d'habitat dans le paysage, sans qu'il n'y ait de perte sensu stricto (Fahrig, 2003). Il est important de noter que la perte et la fragmentation des habitats contribuent à la création d'autres habitats et par conséquent peuvent être favorables à certaines espèces (Bender et al., 1998; Fahrig, 2003). Par exemple, la fragmentation peut être bénéfique pour une espèce associée aux bordures forestières ou à des jeunes stades de succession forestière puisqu'elle augmente la quantité de ces types d'habitats dans le paysage (Andrén, 1994; Fahrig, 2003; Imbeau et al., 2003). Il demeure que la création de bordures n'est avantageuse que pour un nombre restreint d'espèces alors qu'elle pénalise la majorité des communautés forestières (Yahner, 1988; Bosakowski et Smith, 1997).

En plus d'augmenter la quantité de lisières dans le paysage, la fragmentation a pour effet d'accroître le nombre et l'isolement des parcelles d'habitat, de réduire la taille de celles-ci, et d'augmenter la quantité de nouveaux habitats (Andrén, 1994). Il semble que les espèces généralistes s'adaptent plus facilement à ces changements que les spécialistes (McKinney et Lockwood, 1999; Millan de la Pena et al., 2003; Marvier et al., 2004), favorisant ainsi

l'expansion des généralistes dans le paysage au détriment des espèces spécialistes (Bosakowski et Smith, 1997; McKinney et Lockwood, 1999; Millan de la Pena et al., 2003; Marvier et al., 2004). Ainsi, que le changement soit causé par la perte ou la fragmentation des habitats, il aura probablement un impact sur la distribution des espèces dans le paysage.

L'intérêt d'étudier les Strigidés

Étant donné leur nature cryptique et le fait qu'ils soient pour la plupart nocturnes, les Strigidés sont parmi les oiseaux les moins connus. En effet, même les inventaires d'oiseaux à grand déploiement, tels que les atlas des oiseaux nicheurs (e.g., Gauthier et Aubry, 1995), le *Breeding Bird Survey* (Link et Sauer, 1998), ou le recensement des oiseaux de Noël (National Audubon Society, 2002), ne procurent que très peu d'information sur les Strigidés puisque ces inventaires sont habituellement réalisés pendant le jour et à l'extérieur de leur période de reproduction, période où leur détectabilité est plus élevée (Takats et al., 2001).

Pourtant, étant des prédateurs de hauts niveaux trophiques, les Strigidés jouent un rôle fondamental dans les processus écologiques (Molles, 1999). Comme la plupart des oiseaux de proie, ils sont sensibles aux perturbations anthropiques et à la présence de polluants dans l'environnement (Bosakowski et Smith, 1997; Houston et al., 1998; Mazur et James, 2000; Johnsgard, 2002). Il est donc possible de les utiliser comme des « baromètres » pour mesurer la qualité et la santé d'un habitat. De plus, certaines espèces de Strigidés, comme la Chouette rayée (*Strix varia*), sont considérées comme des espèces indicatrices ou parapluie (Rubino et Hess, 2003; Olsen et al., 2006). Une espèce indicatrice est fortement associée à un habitat particulier et représente la qualité de celui-ci (Niemi et al., 1997). En plus d'être indicatrice, une espèce parapluie possède habituellement un large domaine vital dans lequel se trouvent plusieurs autres espèces associées (Roberge et Angelstam, 2004). Ainsi, définir la situation d'une espèce parapluie dans un milieu permet l'évaluation de la situation de plusieurs autres espèces. Par le fait même, en promulguant la conservation d'une espèce parapluie, la conservation des espèces associées devrait également être favorisée (Roberge et Angelstam, 2004).

Interactions entre espèces

Plusieurs études ont tenté de quantifier l'influence de la structure du paysage sur la distribution des Strigidés dans l'espace (e.g., Folliard et al., 2000; Penteriani et al., 2004). Cependant, nulle espèce ne se retrouve complètement isolée des autres. Il est donc primordial de considérer l'impact que les interactions entre espèces peuvent avoir sur cette distribution.

La compétition et la prédation contribuent à contrôler la densité et la distribution d'une population (Molles, 1999). Lorsque le prédateur se nourrit d'une proie, il diminue inévitablement le nombre d'individu de cette population. Cependant, l'effet de la compétition est plus complexe du fait qu'elle peut être intraspécifique ou interspécifique (e.g., Savard, 1982; Essington et al., 2000; Harwood et al., 2002). Elle se produit lorsque deux ou plusieurs individus utilisent les mêmes ressources, par exemple, en ayant une diète similaire, en habitant le même type d'habitat, ou en recherchant les mêmes sites de nidifications (Molles, 1999). Ainsi, les ressources alimentaires semblent être une cause de compétition pour le Garrot d'Islande (*Bucephala islandica*) et le Petit Garrot (*B. albeola*; Savard, 1982), alors que le Saumon de l'Atlantique (*Salmo salar*) et la Truite brune (*S. trutta*) se disputent les refuges disponibles dans le lit d'un cours d'eau (Harwood et al., 2002). Dans les deux cas, cette compétition se produit autant entre individus de la même espèce qu'entre individus d'espèces différentes. Chez les rapaces, la compétition interspécifique se manifeste plus fréquemment entre des espèces de taille similaires (Hakkarainen et Korpimäki, 1996).

La compétition comporte des coûts non négligeables pour l'individu qui la subit. Entre autres, elle diminue les chances de survie et le succès reproducteur des compétiteurs chez plusieurs espèces comme le Gobemouche à collier (*Ficedula albicollis*; Gustafsson, 1987), le Campagnol roussâtre (*Clethrionomys glareolus*; Eccard et Ylonen, 2002), ou le Saumon du Pacifique (*Oncorhynchus sp.*; Essington et al., 2000). Ainsi, deux espèces compétitrices auront communément recours à une ségrégation spatiale ou temporelle afin d'éviter ces effets néfastes. Par exemple, les rapaces peuvent modifier leur niche ou leur horaire de chasse dans le but de diminuer le chevauchement des ressources utilisées et les rencontres agressives entre

compétiteurs (Hakkarainen et Korpimäki, 1996; Vrezec et Tome, 2004ab). Habituellement, le compétiteur dominant parviendra éventuellement à exclure l'autre espèce (Vrezec et Tome, 2004ab). Généralement, la taille est un facteur déterminant dans la sélection d'habitat des Strigidés. En effet, l'espèce de plus grande taille sélectionnera un habitat optimal alors que la seconde se contentera d'un habitat alternatif (Hakkarainen et Korpimäki, 1996; Vrezec et Tome, 2004b). De plus, le Strigidé dominant peut pratiquer la prédation sur le plus petit compétiteur. Comme l'ont souligné Bluhm et Ward (1979), lorsqu'un rapace se nourrit d'un rapace de plus petite taille, il obtient non seulement la nourriture dont il a besoin, mais il élimine également un compétiteur potentiel.

Les interactions entre les différentes espèces de Strigidés peuvent donc influencer l'abondance et la distribution de ceux-ci dans le paysage. De même, les interactions entre espèces pourraient également avoir un impact sur la détectabilité des Strigidés. En effet, un individu ayant entendu son compétiteur ou son prédateur pourrait être moins enclin à chanter afin d'éviter une agression ou la prédation (Kelly et al., 2003; Olson et al., 2005; Crozier et al., 2006). De plus, la densité de la population semble affecter l'activité vocale des Strigidés (Penteriani et al., 2002). Chanter pour défendre son territoire comporte certains coûts puisque, en plus de révéler sa présence aux prédateurs, le temps investi au chant est soustrait au temps disponible pour d'autres activités comme chasser ou se reproduire. Or, Penteriani et al. (2002) ont observé que le Grand-duc d'Europe (*Bubo bubo*) investissait moins d'énergie pour chanter lorsque les voisins étaient inexistants ou lorsqu'ils étaient éloignés. Ainsi, dans une population où la densité est faible, la nécessité de chanter afin de défendre son territoire doit être moins fréquente.

Le recensement des Strigidés

Les Strigidés sont difficiles à recenser puisqu'ils sont nocturnes et qu'ils possèdent de larges territoires à l'intérieur desquels ils peuvent se déplacer rapidement (Fuller et Mosher, 1981; Johnsgard, 2002). Plusieurs techniques d'inventaire ont déjà été utilisées comme les points d'écoute en bordure des routes, les recensements avec lampe de poche (spotlighting), les

transects (walking line-transect) et les recensements en voiture (driving survey; Conway et Simon, 2003; Condon et al., 2005). Cependant, la méthode la plus souvent utilisée est le point d'écoute avec repasse de chant (Takats et al., 2001). Cette méthode se base sur le fait que les Strigidés défendent leur territoire par le chant. La technique consiste à diffuser des enregistrements de chants de Strigidés afin d'inciter les individus présents à répondre à l'appel (Takats et al., 2001). Le point d'écoute avec repasse de chant est donc une méthode qui s'avère très utile auprès d'espèces difficiles à recenser visuellement. De plus, cette technique est très efficace comparativement aux autres méthodes de recensement puisqu'elle permet de détecter un plus grand nombre d'individus par unité de temps (Mosher et al., 1990).

Depuis plusieurs années, des suivis de rapaces nocturnes sont effectués à l'aide de points d'écoute avec repasse de chant un peu partout en Amérique du Nord (Takats et al., 2001; Balej, 2006; Études d'Oiseaux Canada, 2008). Ces recensements sont généralement réalisés par des ornithologues amateurs bénévoles parcourant des routes préétablies par les organisateurs. La plupart du temps, chaque site n'est visité qu'une seule fois par année dans des conditions climatiques favorables. Malheureusement, aucun de ces suivis n'est corrigé pour tenir compte d'une probabilité de détection imparfaite, laquelle peut engendrer des biais lors de l'estimation de l'abondance ou de la distribution d'une espèce (Gu et Swihart, 2004; MacKenzie, 2005a, b). De plus, les repasses de chant incluent plusieurs espèces différentes pour un même point d'écoute. En effet, lors d'une seule visite, les chants de deux à six espèces différentes peuvent être diffusés, une à la suite de l'autre (Takats et al., 2001; Balej, 2006; Études d'Oiseaux Canada, 2008). Considérant les interactions interspécifiques mentionnées plus tôt, une telle pratique pourrait influencer la probabilité de détection des Strigidés. Habituellement, le chant des espèces de plus grande taille est diffusé à la fin du point d'écoute afin de minimiser leur impact sur les plus petites espèces (Takats et al., 2001; Balej, 2006; Études d'Oiseaux Canada, 2008). Bien que cette règle ait été adoptée par la plupart des suivis de rapaces nocturnes, elle n'a jamais été vérifiée.

La probabilité de détection

Les points d'écoute avec repasse de chant sont souvent utilisés pour les collectes de données de type présence-absence. Celles-ci sont appréciées en gestion et en conservation de la faune puisque, comparativement aux données d'abondance, les données de type présence-absence sont obtenues relativement facilement et à coûts moindres (Gu et Swihart, 2004). Cependant, les chercheurs ont souvent prétendu que la détectabilité de pareils recensements était parfaite et qu'un individu présent à un site serait nécessairement détecté (Olson et al., 2005; Vojta, 2005; Wintle et al., 2005). Toutefois, bien qu'il soit possible de confirmer qu'une espèce est présente à un site lorsque celle-ci y est détectée, il est pratiquement impossible de confirmer qu'une espèce est absente (MacKenzie, 2005a, b). En effet, ce qui est considéré comme une absence peut se traduire par deux scénarios : (1) une véritable absence de l'espèce, (2) une fausse-absence où l'espèce occupe le site recensé mais n'a pas été détecté. Ainsi, un site occupé par l'espèce d'intérêt pourrait être considéré inoccupé simplement parce que l'observateur n'a pas été en mesure de détecter l'espèce présente, ou que celle-ci se trouvait ailleurs dans son domaine vital pendant le recensement. Donc, le fait de ne pas détecter une espèce dans une unité d'échantillonnage donnée ne signifie pas nécessairement que celle-ci est absente.

Négliger de tenir compte de la probabilité de détection peut biaiser l'estimation des paramètres dans les modèles de régressions logistiques. Des études effectuées sur les grenouilles et les petits mammifères ont démontré que le fait d'ignorer une détection imparfaite menait à une surestimation ou une sous-estimation de l'influence de certaines variables sur les espèces étudiées (Gu and Swihart, 2004; Mazerolle et al., 2005). Il semble donc nécessaire de considérer la probabilité de détection afin d'obtenir des résultats qui sont justes.

La probabilité de détection peut être influencée par différents facteurs comme les conditions climatiques, le type d'habitat, la région, le moment de l'année, l'heure, la stratégie et l'effort d'échantillonnage, l'espèce, ou même la chance (Takats et al., 2001; Conway et Simon, 2003; Conway et al., 2004; Wintle et al., 2005). D'autres paramètres comme le statut social ou

reproducteur de l'individu, le sexe, l'âge, ou la densité de population peuvent également avoir un impact sur la détectabilité (Penteriani et al., 2002; Wintle et al., 2005). Certains ont même soulevé la possibilité de l'accoutumance à la repasse de chant lorsque cette technique est utilisé trop fréquemment (Haug et Didiuk, 1993; Conway et Simon, 2003). Ainsi, un individu habitué d'entendre des repasses de chant pourrait cesser de répondre à l'appel et compromettre sa détection.

Les conditions météorologiques peuvent affecter le comportement de chant des Strigidés et/ou la capacité de l'observateur à les détecter (Takats et al., 2001). En effet, la probabilité de détection des Strigidés semble diminuer avec des températures très froides et lorsqu'il y a des précipitations (Takats et Holroyd, 1997; Takats et al., 2001). De plus, Hardy et Morrison (2000) ont souligné que de forts vents pouvaient réduire la portée des chants diffusés, diminuer la détectabilité des Strigidés, ou inciter ceux-ci à l'inactivité. Certains chercheurs se sont aussi intéressés à l'influence du couvert nuageux, mais les résultats obtenus sont très variés et aucune tendance réelle n'a pu être observée (Takats et al., 2001).

La taille d'échantillon, la durée des points d'écoute et le nombre de visite à chaque site ont également un impact sur la probabilité de détection des Strigidés (Penteriani et al., 2002). Par exemple, Olson et al. (2005) ont observé qu'une seule visite permettait la détection de seulement 66% des Chouettes tachetées (*S. occidentalis*) présentes, alors que trois visites augmentaient la probabilité de détection à 95%. Selon Dettmers et al. (1999), des points d'écoute d'une durée de cinq à dix minutes seraient suffisants pour recueillir assez de données. De plus, Wintle et al. (2005) croit qu'il serait préférable d'accroître la fréquence des visites à chaque site plutôt que d'augmenter la durée des points d'écoute dans le cas des Strigidés étant donné qu'ils possèdent de très grands domaines vitaux.

Récemment, Hines (2006) a élaboré une méthode permettant d'estimer la probabilité de détection et de corriger l'effet de cette dernière lors de l'estimation de la probabilité d'occurrence (e.g., MacKenzie et al., 2006) ou d'abondance (e.g., Royle, 2004) d'une espèce. Par exemple, à partir de visites répétées au même site, ce logiciel produit un historique de

détection, en indiquant si l'espèce a été détectée (1) ou non (0). Un site visité à trois reprises pourrait, par exemple, avoir un historique de détection de la forme « 010 ». Dans ce cas, l'espèce recensée n'aura été détectée qu'une seule fois, lors de la deuxième visite. Puisqu'au moins une détection a eu lieu, ce site sera considéré comme occupé par l'espèce d'intérêt, mais celle-ci n'aura pas été détectée à la première ni à la troisième visite. En combinant les historiques de détection de chaque site avec les covariables pouvant affecter la détection et la probabilité d'occurrence d'une espèce, il est ainsi possible d'obtenir simultanément la probabilité d'occurrence et la probabilité de détection de cette espèce.

Les objectifs de cette étude

Le but de ce mémoire est de quantifier l'influence de la structure du paysage sur trois espèces de Strigidés, tout en intégrant l'impact des interactions interspécifiques et en tenant compte de la probabilité de détection. Du même coup, je compare l'efficacité de cinq séquences de repasse de chants différentes en estimant la probabilité de détection obtenue pour chacune d'elles. Je compare également les résultats obtenus par des analyses qui ne tiennent pas compte de la probabilité de détection (régressions logistiques) à ceux obtenus par des analyses qui corrigent pour une détection imparfaite (MacKenzie et al., 2002) afin d'évaluer l'importance de considérer la probabilité de détection dans les études sur les Strigidés.

En premier lieu, je m'attends à ce que les espèces spécialistes préfèrent les forêts et évitent les milieux agricoles et les forêts perturbées (Cannings 1993, Mazur and James 2000, Johnsgard 2002). Quant à elles, les espèces généralistes devraient être présentes dans tous les types d'habitats (Bosakowski and Smith 1997, Houston et al. 1998). Pour ce qui est des interactions interspécifiques, je m'attends à ce que la présence d'un prédateur ou d'un compétiteur diminue la probabilité d'occurrence des Strigidés. De plus, l'utilisation de chants de prédateurs lors des recensements devrait diminuer leur probabilité de détection. Finalement, les analyses qui ne tiennent pas compte de la probabilité de détection imparfaite devraient sous-estimer l'occurrence réelle des Strigidés et apporter un biais dans les résultats.

CHAPITRE 1

EFFECTS OF LANDSCAPE ON AN OWL COMMUNITY: ACCOUNTING FOR IMPERFECT DETECTABILITY

Mise en contexte

La présente étude porte sur la probabilité d'occurrence et de détection de trois espèces de Strigidés du Québec, en tenant compte de l'impact possible des interactions interspécifiques sur leur distribution et leur détection. Les auteurs de cette étude sont Geneviève Perreault et Marc Bélisle. Geneviève Perreault est l'auteure qui a le plus contribuée à l'achèvement de cette étude. Elle a trouvé le sujet du projet d'étude, conçu et appliqué le protocole d'échantillonnage sur le terrain, exécuté et interprété la majorité des analyses statistiques des données ainsi que rédigé une version préliminaire complète de cet article. Le présent article est l'objet principal de ce mémoire et sera soumis à la revue The Condor.

ABSTRACT

Although several studies described the influence of landscape structure on landscape or patch occupancy by owls, most did not account for imperfect detection, and overlooked possible interference caused by interspecific interactions. Here, we quantified the influence of landscape structure and species interactions on Great Horned (*Bubo virginianus*), Barred (*Strix varia*) and Northern Saw-whet Owl (*Aegolius acadicus*) occurrence in 2007 and 2008 within 112 sites dispersed across an agriculture-forest gradient in southern Québec, Canada. We also compared the detection probabilities obtained through surveys using single-species broadcasts to those using multiple-species sequences including competitor or predator calls. Finally, we compared the results obtained through simple presence-absence analyses to those obtained when accounting for imperfect detection. Our results showed that, for Great Horned Owl, occupancy was not influenced by landscape composition within a 1-km radius, and detection probability was not affected by call broadcast sequence. On the other hand, Barred and Northern Saw-whet Owl occurrence probability increased with increasing forest cover within a 2-km and 1-km radius, respectively. Overall, the presence of a predator or competitor in the landscape did not seem to influence owl occupancy. However, Great Horned Owl playbacks strongly decreased Barred Owl detection probability. Northern Saw-whet Owl's response to playbacks was not inhibited by Great Horned Owl calls, although its detection probability was higher when using conspecific broadcasts that were free from predator calls. Finally, results showed different landscape relations whether the analyses were performed accounting for imperfect detection or not. More specifically, some variables were significant in only one type of analysis, or the magnitude of the effect differed according to the method used. This study suggests that many parameters may influence owl detection probability, and that imperfect detection should always be accounted for in owl surveys. Moreover, broadcast sequences used in owl surveys should be carefully planned to prevent changes in detection probability caused by species interaction.

INTRODUCTION

The effects of landscape structure on population distribution and abundance may be both direct and indirect (Dunning et al. 1992). First, site occupancy may be the direct result of habitat quality, quantity, or spatial distribution within a hierarchy of spatial scales (Kotliar and Wiens 1990). For instance, most species require a minimum amount of suitable habitat in the landscape to survive (Andrén 1994, Fahrig 2003). Moreover, species distribution and abundance were shown to be influenced by patch size and isolation (Bender et al. 1998, Boulinier et al. 2001, Fahrig 2003), while fragmented landscapes can constrain the movements of birds (Bélisle 2005) and increase the cost of those movements (Hinsley 2000). Second, landscape structure may indirectly influence occupancy through other features like the availability and abundance of food resources, or the occurrence of a predator or competitor. For example, Redpath (1995a, 1995b) reported that landscape structure influenced small mammal density and distribution, which in turn affected Tawny Owl (*Strix aluco*) space use pattern, diet and woodland occupancy. On another front, Kelly et al. (2003) observed that Spotted Owl (*S. occidentalis*) occupancy decreased when Barred Owl (*S. varia*) was detected within 0.8 km of sampling sites. Hence, the occurrence of a species in a given patch or landscape is the result of the combined impacts of direct and indirect effects of landscape structure.

Species are likely to respond differentially to landscape modifications depending on their specific needs. For example, habitat generalists who are more disturbance-tolerant and show higher flexibility are more likely to adapt to landscape change than specialists who have more specific needs (Andrén 1994, Devictor et al. 2008). Hence, landscape disturbance should favor the expansion of generalist species at the detriment of the less flexible specialist ones (McKinney and Lockwood 1999, Marvier et al. 2004). Bosakowski and Smith (1997) suggest, for example, that Great Horned Owls (*Bubo virginianus*), which show low habitat selectivity, may take over forest habitats affected by urban sprawl, while the forest-specialist Barred Owls will avoid those habitats. Moreover, landscape changes can alter species interactions

(Danielson 1991, Danielson 1992, Tylianakis et al. 2008) as predation and interspecific competition may arise, or be amplified between different species. For instance, it has been found that owls tend to use spatial or temporal segregation to decrease overlap in resource use and reduce possible encounters with the competing or predatory species (Hakkarainen and Korpimäki 1996, Vrezec and Tome 2004a, 2004b). In those situations, larger owl species will typically be dominant and exclude the smaller owls (Hakkarainen and Korpimäki 1996, Vrezec and Tome 2004a, 2004b). Hence, such species interactions may arise in owl communities with landscape change.

Quantifying the influence of the multiple pathways through which landscape structure may affect a community of species is complex, especially if targeted species are difficult to monitor. Owls fall into this category given that they are nocturnal and have large territories within which they can move about rapidly (Fuller and Mosher 1981, Johnsgard 2002). One of the most widely used method to survey owls is the call-playback survey in which recordings of owl vocalizations are broadcast in order to elicit a response from individuals that are present (Takats et al. 2001). However, researchers using this method have often assumed perfect detectability, supposing that if a species is present at a given location, it would necessarily be detected (Olson et al. 2005, Vojta 2005, Wintle et al. 2005). Yet, while it may be possible to confirm a species' presence, it is practically impossible to confirm its absence (MacKenzie 2005a, 2005b). Thus, failing to detect a bird does not necessarily mean that it is absent. If not accounted for, imperfect detection could lead to erroneous inferences about owl biology (Gu and Swihart 2004, MacKenzie 2005a, 2005b).

Many owl monitoring programs are using multiple-species broadcast sequences for their surveys. Hence, during a single visit to a site, different owl species' calls (sometimes up to six species) are broadcast consecutively (Takats et al. 2001, Balej 2006, Bird Studies Canada 2008). Considering species interactions, these procedures might not be appropriate since owls' detectability may be affected. Indeed, owls may not respond to call-playback surveys if they previously hear the call of another species from which they are vulnerable to harassment or predation (Kelly et al. 2003, Olson et al. 2005, Crozier et al. 2006).

In this study, we assess the influence of landscape structure on the occurrence of different owl species in southern Québec, accounting for an imperfect detection probability. We also measure the influence of species interactions on landscape occupancy pattern. Furthermore, to address the possible influence of multiple-species broadcast sequences on owl detectability, we test five different calling sequences. We compare the detection probabilities obtained through surveys using single-species broadcasts to those using multiple-species sequences in which a predator call is previously broadcast. Finally, we repeat our landscape analysis using simple presence-absence analyses (logistic regressions) to quantify the impact of not accounting for imperfect detection when assessing the influence of environmental covariates on species occurrence.

We predict that specialist species should occupy mostly forest habitats and avoid agriculture and disturbed forests (Cannings 1993, Mazur and James 2000, Johnsgard 2002), while generalists might be present in any kind of habitats (Bosakowski and Smith 1997, Houston et al. 1998). We also predict that the presence of a predator will decrease the occurrence probability of a prey species, and that competition will lower the occurrence probability of the more vulnerable species. Moreover, we expect that broadcasting the calls of a predator will decrease the detection probability of owls. Finally, we believe that analyses that do not account for imperfect detection will underestimate the actual occupancy of owls and introduce a bias in the results.

METHODS

Model species

In this study we focus our attention on three of the most common owl species found in southern Québec: Great Horned Owl, Barred Owl and Northern Saw-whet Owl (*Aegolius*

acadicus). Great Horned Owl prey on the other two species and overlap in breeding habitat (Cannings 1993, Houston et al. 1998, Mazur and James 2000, Johnsgard 2002). Moreover, Barred Owl compete over food resources with both species and with Northern Saw-whet Owl for breeding sites (Mazur and James 2000, Johnsgard 2002). Finally, we compare a generalist (Great Horned Owl) with two specialist (Barred and Northern Saw-whet Owl) species to contrast their responses to landscape change.

Great Horned Owl (GHOW)

Great Horned Owl is a permanent resident of all forested habitats with the most extensive range reaching up to the northern tree limit (Houston et al. 1998, Johnsgard 2002). They are found in open and secondary-growth woodlands near fields and open areas (Houston et al. 1998, Johnsgard 2002) where they feed on a broad variety of preys mostly composed of mammals and birds (Rudolph 1978, Houston et al. 1998). Great Horned Owl seems to benefit from heterogeneous and human altered habitats, and make use of edges and fragmented landscapes (Bosakowski and Smith 1997, Houston et al. 1998, Grossman et al. 2008). They are monogamous and show high level of site fidelity with pairs occupying and defending their territory year-round (Houston et al. 1998). Old open nests of hawks, crows, or squirrels are commonly used close to forest edges, human structures or water (Houston et al. 1998, Smith et al. 1999).

Barred Owl (BDOW)

Barred Owl is a permanent resident associated with large blocks of unfragmented mature forest where cavities can be found for nesting (Haney 1997, Postupalsky et al. 1997, Mazur et al. 1998, Olsen et al. 2006, Grossman et al. 2008). Some authors suggest that this preference for undisrupted forests may be due to fewer Great Horned Owls using these habitats, and thus reducing competition and predation (Takats 1998). They seem to prefer forests with dense canopy cover as it presumably protects them against predators and mobbing, and facilitates thermoregulation (Laidig and Dobkin 1995, Haney 1997, Mazur and James 2000). They also appear to avoid young forests, open areas and suburban habitats (Mazur and James 2000, Hinam and Duncan 2002). Barred Owl is often found near wetlands (e.g.: marshes, swamps)

and riparian habitats (Mazur et al. 1997, Mazur and James 2000, Hinam and Duncan 2002). They are monogamous and defend their territory throughout the year (Mazur and James 2000, Johnsgard 2002). Finally, Barred Owl is an opportunistic predator feeding on small mammals and birds as well as amphibians, reptiles, fish and invertebrates (Mazur and James 2000, Johnsgard 2002).

Northern Saw-whet Owl (NSWO)

Unlike the other species, Northern Saw-whet Owl is not a permanent resident. Although some individuals may be present throughout the year, most migrate south for winter (Cannings 1993, Marks and Doremus 2000). Having irregular movement patterns, it is difficult to tell exactly when and where they are going, however some individuals are thought to move as far as southeastern United States (Cannings 1993, Brinker et al. 1997). Northern Saw-whet Owl is found in most woodland habitats but seems to prefer dense and humid coniferous or mixed-wood forests (Cannings 1993, Johnsgard 2002). They appear to benefit from edges along which they forage for small mammals, birds and insects (Cannings 1993, Johnsgard 2002). However, Grossman et al. (2008) found they were more abundant in more connected landscapes. Northern Saw-whet Owl is seasonally monogamous although females may practice sequential polyandry (Cannings 1993, Johnsgard 2002). They breed in mature and old growth forests where woodpeckers' cavities can be found since they are obligate secondary cavity nesters (Cannings 1993, Johnsgard 2002).

Study area

This study was conducted within a ca. 7950-km^2 area in the Eastern Townships, southern Québec, Canada (Fig. 1), mainly composed of mixed and deciduous forests and agricultural lands, interspersed with a few water bodies and urban areas. The landscape is thus dominated either by forest or agriculture. A total of 112 broadcasting stations were selected at random respecting specific criteria. All sites were located along low-traffic roads that are easily accessible in winter and spaced at least 4 km apart from each other to avoid contacting the

same bird. Stations also needed to keep a minimum 200-m distance from nearby houses to avoid disturbing the owners and reduce interference from dog barking. We selected sites that allowed the coverage of a large agriculture-forest gradient (i.e., 20% to 80% agriculture within a 2-km radius) to compare agriculture versus forest-dominated landscapes (Fig. 2).

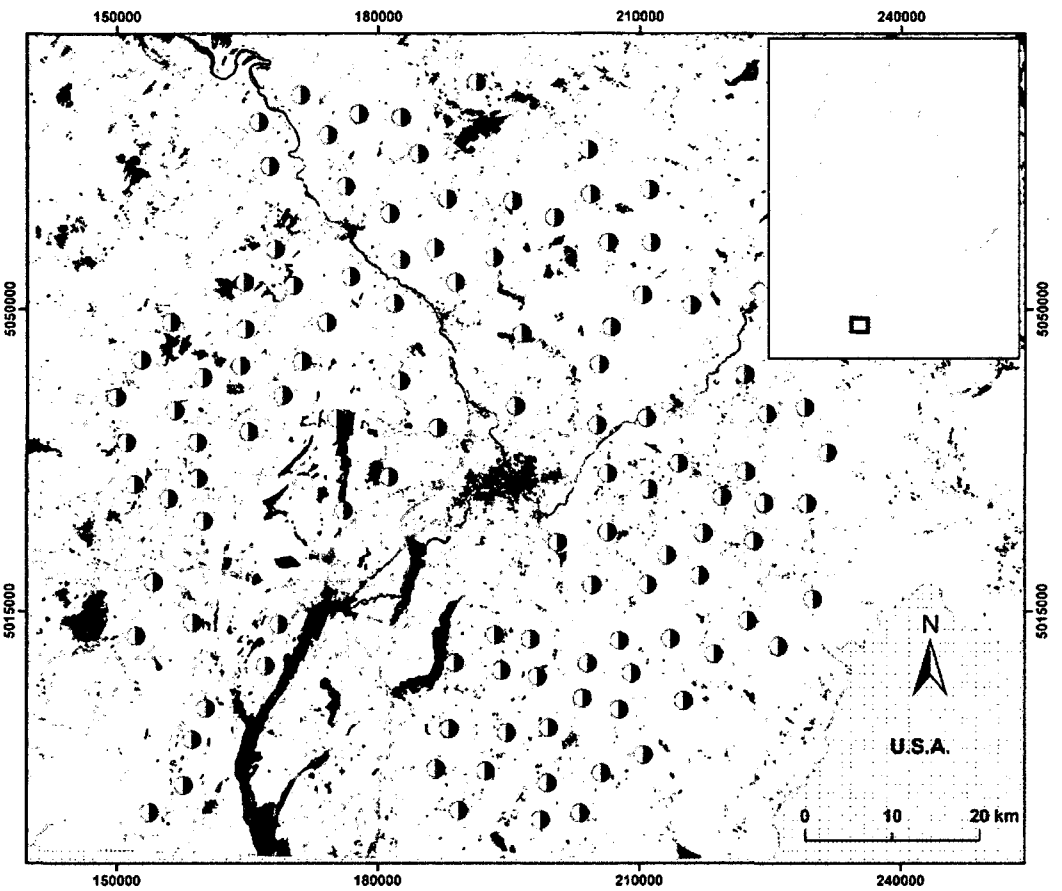

FIG. 1. Distribution of the 112 sites surveyed for owls in 2007-2008 in southern Québec, Canada. Black and white circles indicate site locations. Land cover types include forest (white), disturbed forest (light gray), agriculture (mid-tone gray), urban (dark gray), and water (black). Coordinate units are UTM.

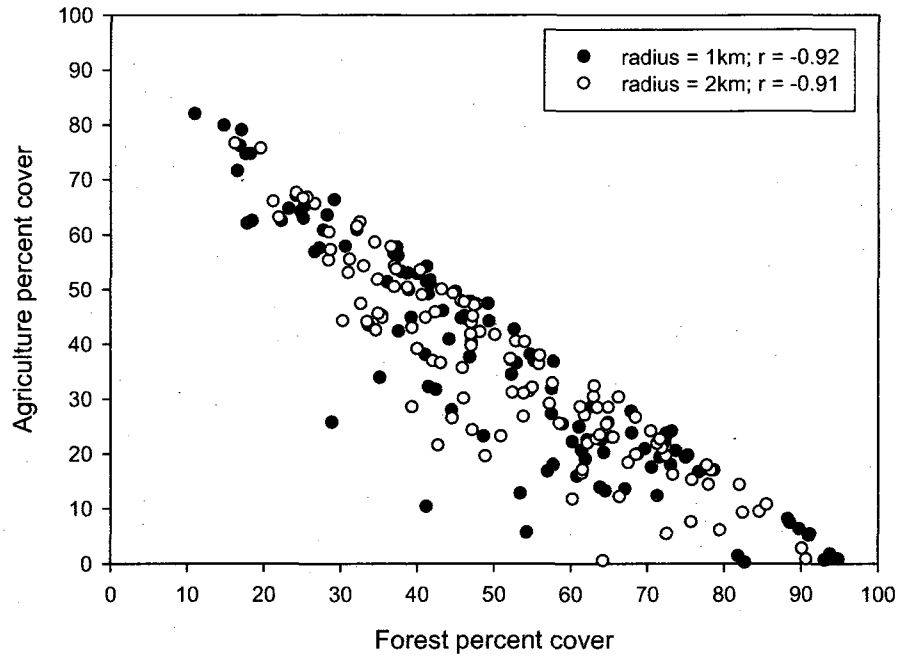

FIG. 2. Relationship between agriculture and forest covers within 1km and 2km radii for the 112 survey sites in southern Québec, Canada (Fig. 1).

Sampling design

Playbacks

We conducted owl surveys through call-playbacks over two consecutive years (2007-2008). The different calling sequences used for these surveys were created using existing recorded territorial calls. Vocalizations from the *Voices of North American Owls* compact disc (Macaulay Library, Cornell Laboratory of Ornithology, 2006) were used for Great Horned (male-female duet from track #44: Territorial hooting or advertisement song) and Northern Saw-whet (track #61: Male advertising song) Owls. For Barred Owls, the "Who cooks for you, who cooks for you all" phrase was acquired from the *Les sons de nos forêts* compact disc (Centre de conservation de la faune ailée de Montréal, 1991 [track #41: Chouette rayée]).

We broadcast the calling sequences using an mp3 player (m230 Sansa, SanDisk) and portable sound system (Pignose Lil'PA). The volume of both devices was adjusted to the maximum possible level without distortion. Field tests (n = 5 per species) revealed that our broadcasts could be heard 1070 to 1470 m away by human ear in open areas (GHOW (mean ± SD): 1110 ± 33.9 m; BDOW: 1416 ± 11.4 m; NSWO: 1458 ± 17.9 m).

Five calling sequences were used: three single species broadcasts ((1) GHOW only, (2) BDOW only, (3) NSWO only) and two Great Horned Owl-treatment broadcasts ((1) GHOW+BDOW, (2) GHOW+NSWO). The single species broadcasts began with one minute of silence allowing the observer to get used to the listening environment. A soft tonality was then heard to indicate the start of data recording. The next minute was silent in order to listen for spontaneously calling individuals. It was followed by a ca. 20 seconds calling bout during which one vocalization was broadcast at 45, 135, 225 and 315 degrees from the road (in the case of NSWO, the continuous 20-s call was broadcast for 5s in every direction). This was followed by one minute of silence to listen for responding individuals. This calling-listening sequence was repeated six times and ended with a final 2-min silent listening period. The end of data recording was then marked with a loud tonality. For the GHOW-treatment broadcasts we used the same calling sequence, preceded by one minute of silent listening and two minutes of continuous GHOW calls, after which the official data recording period began. The total survey (data recording) duration was 10 min for GHOW, NSWO and GHOW+NSWO broadcasts, and 10.5 min for BDOW and GHOW+BDOW broadcasts.

Owl surveys

We tested each of the 5 calling sequences twice at every site, for a total of 10 visits per site per year. All surveys were conducted from one hour to nine hours after sunset. Survey routes were planed to limit the instances where a site would be visited at the same hour twice. All data were collected under good weather conditions: temperature $\geq$ -25°C, wind $\leq$ 15km/h, and with no or very light precipitations (Appendix 1). A minimum 7-day interval separated each visit to the same site so as to avoid owls' habituation to broadcasts. For both years, surveys were performed by two observers working on their own. Each observer visited every site and

broadcast every calling sequence at random dates and hours. Only one observer conducted surveys in both years.

The calling sequences were broadcast according to the owls' calling activity pattern. Great Horned Owls seem to be more vocally active during the month of December through March (Johnsgard 2002), while Barred Owls are mostly heard through the months of February to April, with a peak in late March and April (Mazur and James 2000, Johnsgard 2002). Although Great Horned and Barred Owls may be heard throughout the year, Northern Saw-whet Owls are only vocally active between March and May since they remain mute while wintering and during migration (Johnsgard 2002). Hence, GHOW, BDOW and GHOW+BDOW calling sequences were broadcast randomly between 1 February and 30 May in 2007 and between 14 January and 20 May 2008. NSWO and GHOW+NSWO calling sequences were broadcast randomly after the first Northern Saw-whet Owls were detected in the field: between 23 March and 30 May in 2007 and between 10 March and 20 May 2008.

Data collection

Every time an owl was detected, we recorded the species, the minimum possible number of individuals, and the type of detection (auditory or visual). For each visit, we also recorded the Julian date, hour, temperature, wind speed, and noise level. Temperature (±1°C) and wind speed (±3% of reading) were measured using a Kestrel 2000 Pocket Weather Meter (Nielsen-Kellerman). To estimate noise level, we developed an index that combines two types of distraction: car disturbance and background noise. First, we counted each car that drove beside us during the survey and multiplied this number by 4 to get the car disturbance level. Then, each background noise heard during the survey was recorded into a category: background circulation, snowmobiles, wind, running water, dogs, frogs or other. Each noise was further classified into frequency (never: 0, punctual: 1, intermittent: 2, constant: 4) and intensity (silence: 0, soft: 1, moderate: 2, loud: 3) levels. For each noise category, we multiplied the values attributed to frequency and intensity to get the noise level of each category. Noise levels of every category were then added to obtain the total background noise. Finally, the previously estimated car disturbance level was added to the total background noise to get the

survey's total noise level estimation. Although we are aware this noise index is arbitrary, we think it is representative of the noise disturbance experienced during the survey. Since it was demonstrated that background noise decreases detection probability (Pacifici et al. 2008), we thought it was important to consider it in our analysis.

Landscape characterization

Land cover of the study area was obtained through georeferenced, classified Landsat-7 satellite images taken between August 1999 and May 2003 (resolution: 25 m × 25 m; Canadian Wildlife Service 2004). We divided land cover into six categories: (1) forest (deciduous, mixed and coniferous woodlands), (2) disturbed forest (regenerations, burns, cuts), (3) agriculture (croplands, pastures, hayfields, fallows), (4) water (rivers, lakes), (5) wetland (bogs, swamps, marshes), and (6) urban (roads, bare ground, airports, borrow pit, quarry, golf, urban parks, villages, cities) using ArcView GIS Spatial Analyst 2.0 (ESRI 2005). FRAGSTATS 3.3 (McGarigal et al. 2002) was used to calculate the percent cover of every category around each site within a 1-km radius for Great Horned and Northern Saw-whet Owls and a 2-km radius for Barred Owls. We chose the radii based on the owls' home range size. We estimated the average home range radii to be ~0.72km for Great Horned Owls (Houston et al. 1998), ~1.13km for Barred Owls (Mazur and James 2000), and ~0.69km for Northern Saw-whet Owls (Cannings 1993). Since our sites had little chance of being situated at the center of the owl's actual home range, we found it would be suitable to double those radii so as to ensure the analyzed area would encompass as much of the home range as possible. In addition, when choosing a territory, owls may also consider surrounding habitats and the presence of conspecifics (Addicott et al. 1987, Dunning et al. 1992, Andrén 1994). Thus, doubling the radii allowed us to include some of the home range's surrounding habitats into the analysis.

Statistical analyses

In addition to our three study species, the presence of one Eastern Screech-Owl (*Megascops asio*) individual was recorded on five visits at the same site in 2007 and once at a neighboring site in 2008. However, only Great Horned, Barred and Northern Saw-whet Owls were considered for data analysis. Furthermore, the number of surveyed owls per visit was low (mostly 1 or 2), preventing us from achieving abundance analysis. Hence the minimum possible number of individuals was converted into simpler presence-absence (0 or 1) data. We estimated the occurrence of owls using PRESENCE 2.2 (Hines 2006) which allows simultaneous estimation of occurrence and detection probability following MacKenzie et al. (2002). A single-species analysis was performed separately for each year and each species. Although multiple-species or multiple-season analyses would have been more appropriate, these model types did not converge. In fact, the method proposed by MacKenzie et al. (2002) to account for imperfect detection uses complex algorithms that are sensitive to colinearity problems. Hence, a very low detection probability or an increase in the number of variables in a model may lead to convergence problems.

Assumptions

Four assumptions had to be followed in single-species analysis (MacKenzie et al. 2006). First, the sites are considered "closed" to changes in occupancy during the entire sampling season (i.e.: no extinctions or colonizations). In this study, the analyses were performed separately for the two years of data collection. Moreover, since our surveys were performed during the breeding season, when owls remain within the same territory and actively defend it from intruding individuals (Johnsgard 2002), we are confident that this first assumption was met. Second, the probability of occupancy is the same for all sites, and third, the probability of detection, given the species is present, is constant across all sites. These two assumptions can be relaxed if differences in occupancy and detection probabilities are modeled as function of covariates (e.g., including a forest cover variable when estimating occupancy and a temperature variable for detection), which is what was done here. Finally, detection histories and detection of species at each site are independent. Given that our sites were spaced so as to

prevent double-sampling and that each visit to the same site was achieved with a minimum 7-day interval, we feel secure that this last assumption was respected.

Models

For each owl species, we built a series of models that shared a fixed set of detection covariates combined with a variety of occurrence covariates (Table 1 and 2). All detection and occurrence covariates were centered on the mean to ease convergence of models. Nevertheless, convergence was not reached for Great Horned Owl 2007 and Northern Saw-whet Owl 2008 possibly due to low detection probability. Thus, only Barred Owl was analyzed in both years. Moreover, one site was removed each from the Barred Owl 2008 and Great Horned Owl 2007 analyses since exceptionally high detection rates occurred at these sites, preventing proper model fitting. For any given model, Pearson product-moment correlations (r) among explanatory variables ranged between -0.53 and 0.41 with the exception of Julian day and temperature which were strongly correlated ($0.75 < r < 0.82$). However, we decided to keep both variables since they are both believed to influence owl detectability (Takats and Holroyd 1997, Takats et al. 2001) and did not cause colinearity problems when estimating parameters. To be sure, we compared the values of a model including both variables with a model including either Julian day or temperature. When both variables were included in the model, the standard errors were not inflated.

TABLE 1. Explanatory variables used to assess the occurrence and detection probability of Great Horned (GHOW), Barred (BDOW) and Northern Saw-whet (NSWO) Owl in 2007 and 2008 within agricultural landscapes of southern Québec, Canada.

Variable	Abbreviation	Justifications	Species
Occurrence			
Forest cover (%) [A]	for	Important for nesting, roosting, and foraging (Johnsgard 2002)	All
Disturbed forest cover (%)	disturb	Should be avoided by BDOW and NSWO (Cannings 1993, Mazur and James 2000, Johnsgard 2002)	All
Wetland cover (%) [B,C]	wet	Often associated with BDOW and NSWO (Cannings 1993, Mazur and James 2000, Johnsgard 2002)	All
Great Horned Owl occurrence	GHOWocc	BDOW and NSWO should avoid habitats where GHOW is present since it is their predator and competitor (Cannings 1993, Bosakowski and Smith 1998, Houston et al. 1998, Mazur and James 2000, Johnsgard 2002)	BDOW, NSWO
Barred Owl occurrence	BDOWocc	NSWO might avoid habitats where BDOW is present since they are competitors (Mazur and James 2000, Johnsgard 2002)	NSWO
Detection			
BDOW broadcast [D]	bBDOW	To compare efficiency of single- and multiple-species broadcasts	All
NSWO broadcast [D]	bNSWO	To compare efficiency of single- and multiple-species broadcasts	All
GHOW+BDOW broadcast [D]	bGH_BDOW	To compare efficiency of single- and multiple-species broadcasts	All
GHOW+NSWO broadcast [D]	bGH_NSWO	To compare efficiency of single- and multiple-species broadcasts	All
Date (Julian day) [A]	julian	Calling activity of owls may change according to time of year (Takats et al. 2001, MacKenzie 2005b)	All
Time since sunset (hour)	postsun	Calling activity of owls may change according to time of day (Takats and Holroyd 1997)	All
Temperature (°C)	temp	Calling activity of owls may decrease in cold temperatures (Takats and Holroyd 1997)	All
Noise level [E]	noise	Detection of owls decrease with background noise (Pacifici et al. 2008)	All
Observer	obs	Detection of owls may vary between different observers (Sauer et al. 1994)	All

[A] These variables were also squared to account for possible quadratic relations.
[B] This variable was considered in interaction with the amount of forest cover because the effect of forest cover may be amplified by additional wetland cover.
[C] This variable represents both the water (rivers, lakes) riparian habitats and the wetlands (bogs, swamps, marshes). It was computed as the sum of the wetland percent cover and the water total edge percent cover (water total edge (m) × 30 (m)/ area (m^2)). We used 30 m assuming edge effect can be observed up to 30 meters into a patch (Matlack and Litvaitis 1999).
[D] These variables are dummy variables for the calling sequences used, with the GHOW broadcast set as the reference calling sequence.
[E] Noise index on a level of 1 to 44, see the Methods section for further explanations.

TABLE 2. Model selection for owl occupancy in agricultural landscapes of southern Québec, Canada, using two different types of analyses. Models accounting for imperfect detection probability (MacKenzie et al. 2002) shared the following additional detection covariates: bBDOW + bNSWO + bGH_BDOW + bGH_NSWO + julian + julian^2 + postsun + temp + noise + obs. See Table 1 for definitions of variables.

	2007				2008			
	MacKenzie et al. (2002)		Logistic regression		MacKenzie et al. (2002)		Logistic regression	
Model	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i
Great Horned Owl								
(1) for + for^2			0.000	0.4672	4.318	0.0965	0.000	0.4316
(2) for + for^2 + disturb			1.829	0.1873	6.878	0.0268	2.150	0.1473
(3) for + for^2 + wet			2.071	0.1659	6.968	0.0256	1.316	0.2235
(4) for + for^2 + disturb + wet			3.998	0.0633	9.605	0.0069	3.436	0.0774
(5) for + for^2 + wet + for × wet			3.382	0.0861	9.685	0.0066	3.160	0.0889
(6) for + for^2 + disturb + wet + for × wet			5.479	0.0302	12.389	0.0017	5.252	0.0312
(7) Detection variables only					0.000	0.8359		
Barred Owl								
(1) for + for^2	2.466	0.1236	2.625	0.0995	0.000	0.3889	0.247	0.2028
(2) for + for^2 + disturb	3.570	0.0712	3.761	0.0564	2.670	0.1023	1.596	0.1033
(3) for + for^2 + wet	5.211	0.0313	4.775	0.0340	2.256	0.1259	1.822	0.0923
(4) for + for^2 + disturb + wet	6.286	0.0183	5.930	0.0191	3.230	0.0773	3.390	0.0421
(5) for + for^2 + wet + for × wet	0.000	0.4241	0.000	0.3698	4.101	0.0500	0.000	0.2295
(6) for + for^2 + disturb + wet + for × wet	4.041	0.0562	2.164	0.1253	5.006	0.0318	2.208	0.0761
(7) for + for^2 + GHOWocc	3.540	0.0722	4.305	0.0430	2.350	0.1201	2.299	0.0727
(8) for + for^2 + disturb + GHOWocc	6.076	0.0203	5.471	0.0240	5.066	0.0309	3.705	0.0360
(9) for + for^2 + wet + GHOWocc	7.875	0.0083	6.497	0.0144	5.021	0.0316	3.969	0.0315
(10) for + for^2 + disturb + wet + GHOWocc	8.851	0.0051	7.663	0.0080	5.956	0.0198	5.580	0.0141
(11) for + for^2 + wet + for × wet + GHOWocc	2.320	0.1330	1.739	0.1550	6.945	0.0121	2.233	0.0751
(12) for + for^2 + disturb + wet + for × wet + GHOWocc	4.926	0.0361	3.940	0.0516	7.791	0.0079	4.484	0.0244
(13) Detection variables only	14.882	0.0002			11.302	0.0014		
Northern Saw-whet Owl								
(1) for + for^2	7.264	0.0084	2.559	0.0854			2.314	0.0682
(2) for + for^2 + disturb	7.364	0.0080	3.136	0.0640			0.578	0.1624
(3) for + for^2 + wet	0.064	0.3074	0.000	0.3069			2.580	0.0597
(4) for + for^2 + disturb + wet	0.000	0.3174	1.567	0.1402			1.838	0.0865
(5) for + for^2 + wet + for × wet	2.000	0.1168	1.012	0.1851			0.000	0.2168
(6) for + for^2 + disturb + wet + for × wet	2.434	0.0940	2.469	0.0893			0.026	0.2141
(7) for + for^2 + GHOWocc + BDOWocc	9.480	0.0028	6.280	0.0133			4.154	0.0272
(8) for + for^2 + disturb + GHOWocc + BDOWocc	10.154	0.0020	6.617	0.0112			2.916	0.0504
(9) for + for^2 + wet + GHOWocc + BDOWocc	3.674	0.0505	3.806	0.0458			4.950	0.0182
(10) for + for^2 + disturb + wet + GHOWocc + BDOWocc	4.069	0.0415	5.282	0.0219			4.538	0.0224
(11) for + for^2 + wet + for × wet + GHOWocc + BDOWocc	5.259	0.0229	5.039	0.0247			3.459	0.0385
(12) for + for^2 + disturb + wet + for × wet + GHOWocc + BDOWocc	6.295	0.0136	6.425	0.0124			3.616	0.0356
(13) Detection variables only	6.135	0.0148						

Model selection and multi-model inference

We contrasted models based on the Akaike information criterion, corrected for small sample size (AIC_c) following Burnham and Anderson (2002). Since none of the models were neatly superior to the others ($w_i > 0.95$), we performed multi-model inference (Burnham and Anderson 2002). We also calculated the unconditional standard errors and 95% confidence intervals associated with each covariate (Burnham and Anderson 2002). Model goodness-of-fit was assessed following MacKenzie and Bailey (2004) using the most complex model of the set.

Logistic regressions

Wishing to compare the results of analyses that account for detection probability and others that do not, we ran a second version of our analyses using logistic regressions in the R statistical environment (version 2.9.0; R Development Core Team 2009). The same models were used and compared through AIC_c before performing model averaging.

RESULTS

Under average conditions (Appendix 1), detection probability was relatively low for all species when using conspecific calls (range: 0.11-0.32; Table 3). On the other hand, the occurrence probability was fairly high for all species in average landscapes (Appendix 2) without predators or competitors, (range: 0.43-0.94; Table 3). Northern Saw-whet Owl had the highest occurrence probability and Great Horned Owl the lowest. Occurrence probabilities were 0.13 to 0.49 higher than naïve occupancy estimates as it was expected since detection probabilities were < 1 for all species (Table 3). Interestingly, for Barred Owl, occupancy was higher in 2008 but if detection probability was ignored, occupancy would mistakenly have been considered higher in 2007.

TABLE 3. Detection and occurrence probabilities of owls in southern Québec as estimated following MacKenzie et al. (2002). Naïve occupancy estimates (i.e., not corrected for imperfect detection) are also presented. These estimates were obtained under average conditions (Appendices 1 and 2) and using conspecific calls in an average landscape without predator or competitor.

	Great Horned Owl		Barred Owl		Northern Saw-whet Owl	
	2007	2008	2007	2008	2007	2008
Detection probability (p)		0.166	0.317	0.112	0.230	
Naïve occupancy estimate	0.330	0.304	0.545	0.491	0.455	0.179
Occurrence probability (ψ)		0.434	0.679	0.881	0.942	

TABLE 4. Effects of detection probability covariates obtained following MacKenzie et al. (2002) and subjected to multi-model inference. Regression coefficients (θ) are shown with their unconditional standard errors (SE) and 95% confidence intervals. Note that all values are expressed in logit. See Table 1 for definitions of variables and Table 2 for the set of models.

Parameter	Beta (θ)	SE	95% CI	Beta (θ)	SE	95% CI
	Great Horned Owl 2008			**Northern Saw-whet Owl 2007**		
intercept (p)	**-1.614**	**0.420**	**-2.436 < θ < -0.791**	**-2.544**	**0.419**	**-3.366 < θ < -1.723**
bBDOW	-1.134	0.614	-2.338 < θ < 0.070	-0.846	0.627	-2.075 < θ < 0.382
bNSWO	-0.517	0.572	-1.639 < θ < 0.604	**1.335**	**0.460**	**0.434 < θ < 2.236**
bGH_BDOW	-0.149	0.472	-1.073 < θ < 0.776	-0.391	0.552	-1.472 < θ < 0.690
bGH_NSWO	0.613	0.508	-0.382 < θ < 1.608	**1.181**	**0.467**	**0.264 < θ < 2.097**
julian	-0.002	0.009	-0.019 < θ < 0.015	**-0.020**	**0.008**	**-0.036 < θ < -0.003**
julian^2	0.000	0.000	-0.001 < θ < 0.000	0.000	0.000	-0.001 < θ < 0.000
postsun	**0.217**	**0.086**	**0.048 < θ < 0.386**	-0.118	0.074	-0.263 < θ < 0.027
temp	0.020	0.030	-0.038 < θ < 0.077	**0.071**	**0.028**	**0.016 < θ < 0.126**
noise	-0.015	0.029	-0.073 < θ < 0.042	**-0.072**	**0.027**	**-0.125 < θ < -0.018**
obs	-0.096	0.306	-0.697 < θ < 0.504	0.169	0.261	-0.342 < θ < 0.680
	Barred Owl 2007			**Barred Owl 2008**		
intercept (p)	**-1.996**	**0.317**	**-2.618 < θ < -1.375**	**-3.189**	**0.399**	**-3.970 < θ < -2.407**
bBDOW	**1.229**	**0.362**	**0.519 < θ < 1.938**	**1.117**	**0.457**	**0.222 < θ < 2.013**
bNSWO	-0.088	0.380	-0.833 < θ < 0.658	0.513	0.458	-0.386 < θ < 1.411
bGH_BDOW	0.436	0.383	-0.316 < θ < 1.187	0.882	0.468	-0.035 < θ < 1.800
bGH_NSWO	-0.221	0.384	-0.973 < θ < 0.532	0.138	0.474	-0.791 < θ < 1.067
julian	**0.031**	**0.006**	**0.019 < θ < 0.043**	**0.024**	**0.006**	**0.012 < θ < 0.036**
julian^2	0.000	0.000	-0.000 < θ < 0.000	**0.000**	**0.000**	**0.000 < θ < 0.001**
postsun	0.005	0.060	-0.113 < θ < 0.123	0.077	0.066	-0.052 < θ < 0.206
temp	-0.016	0.023	-0.060 < θ < 0.029	0.002	0.025	-0.047 < θ < 0.051
noise	**-0.055**	**0.023**	**-0.100 < θ < -0.010**	**-0.085**	**0.027**	**-0.139 < θ < -0.031**
obs	**-0.607**	**0.217**	**-1.032 < θ < -0.182**	-0.267	0.239	-0.736 < θ < 0.202

Effects of covariates on detection

GHOW 2008

The detectability of Great Horned Owl was not affected by the type of broadcast used during the survey (Table 4). However, the odds of detecting a Great Horned Owl increased by 24.3% ($100(e^{0.217}-1) = 24.3\%$) with every 1-hour increase after sunset (Table 4 and Fig. 3). Surprisingly, noise level did not seem to influence Great Horned Owl's detection (Table 4). Likewise, date, temperature and observer did not have an effect on the detection probability of this species (Table 4).

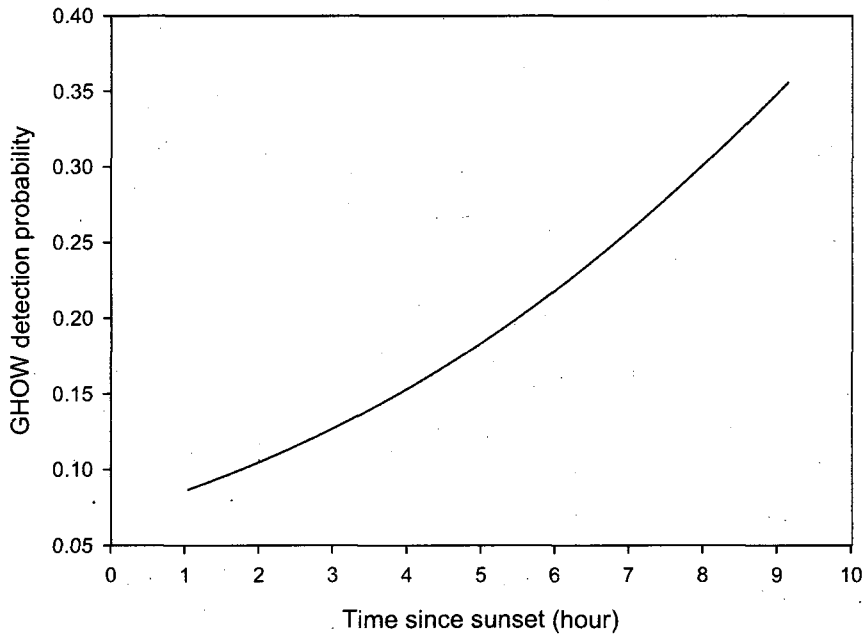

FIG. 3. Effect of time of night (postsun) on Great Horned Owl detectability in 2008 within agricultural landscapes of southern Québec, Canada. Predicted values were obtained following MacKenzie et al. (2002) and multi-model inference (see Table 4) under average conditions (Appendices 1 and 2) when using conspecific calls in an average landscape without predator or competitor.

BDOW 2007-2008

The odds of detecting a Barred Owl were much higher (by 242% in 2007; 206% in 2008) when using the BDOW broadcast compared to when using the GHOW broadcast (Table 4). Moreover, in both years, surveys using the GHOW and GHOW+BDOW broadcasts showed similar detection probabilities (Table 4). Hence, if the GHOW broadcast was heard first, the BDOW broadcast did not increase Barred Owl detection probability. This clearly shows the negative impact of Great Horned Owls' calls on Barred Owl's detectability. The odds of detecting a Barred Owl increased slightly throughout the season (by 3.2% in 2007; 2.4% in 2008, for every one-day increase; Table 4). More specifically, detection probability increased steadily from 0.1 to 0.8 throughout the season under average conditions (Appendix 1) in 2007. However, it remained stable at ~0.1 for the first half of the 2008 season and increased rapidly up to 0.7 for the second half. In both years, detection of Barred Owl decreased with increasing noise, but was not affected by time elapsed after sunset (postsun), or temperature (Table 4). Finally, an observer effect was detected in 2007 only. That year, the odds of detecting a Barred Owl were 46% lower for observer 2 compared to the first observer (Table 4).

NSWO 2007

The odds of detecting a Northern Saw-whet Owl were a lot higher when using the NSWO and GHOW+NSWO broadcasts compared to when using the GHOW broadcast (NSWO: 280%; GHOW+NSWO: 226%; Table 4). Hence, Northern Saw-whet Owl's response to playbacks was not inhibited by Great Horned Owl calls, although its detection probability was higher when using conspecific broadcasts that were free of predator calls (Table 4). While their detection probability remained stable throughout the night (postun), the odds of detecting a Northern Saw-whet Owl decreased as the breeding season progressed (1.9% decrease per one-day increase; Table 4). On the other hand, the odds of detecting a Saw-whet increased by 7.4% with every one-degree increase in temperature (Table 4). Finally, the detection probability of Northern Saw–wet Owls decreased with noise, as expected, and there were no significant observer effect for this species (Table 4).

TABLE 5. Effects of occupancy covariates obtained when accounting for imperfect detection (MacKenzie et al. 2002) or through logistic regressions and subjected to multi-model inference. Regression coefficients (θ) are shown with their unconditional standard errors (SE) and 95% confidence intervals. Note that all values are expressed in logit. See Table 1 for definitions of variables and Table 2 for the set of models.

	MacKenzie et al. (2002)			Logistic regression		
Parameter	**Beta (θ)**	**SE**	**95% CI**	**Beta (θ)**	**SE**	**95% CI**
Great Horned Owl 2007						
intercept (ψ)						
for				-0.002	0.009	$-0.020 < \theta < 0.017$
for^2				0.000	0.000	$-0.001 < \theta < 0.001$
disturb				0.016	0.030	$-0.043 < \theta < 0.075$
wet				0.013	0.073	$-0.130 < \theta < 0.155$
for × wet				-0.004	0.005	$-0.015 < \theta < 0.006$
Great Horned Owl 2008						
intercept (ψ)	-0.264	0.331	$-0.914 < \theta < 0.385$			
for	-0.008	0.012	$-0.033 < \theta < 0.016$	-0.005	0.009	$-0.023 < \theta < 0.014$
for^2	0.000	0.001	$-0.001 < \theta < 0.002$	0.000	0.000	$-0.001 < \theta < 0.001$
disturb	-0.013	0.038	$-0.088 < \theta < 0.062$	-0.005	0.031	$-0.066 < \theta < 0.056$
wet	-0.011	0.090	$-0.187 < \theta < 0.165$	0.064	0.073	$-0.078 < \theta < 0.206$
for × wet	0.000	0.007	$-0.013 < \theta < 0.014$	-0.003	0.004	$-0.011 < \theta < 0.006$
Barred Owl 2007						
intercept (ψ)	0.751	0.422	$-0.075 < \theta < 1.578$			
for	**0.085**	**0.028**	**$0.029 < \theta < 0.140$**	**0.065**	**0.021**	**$0.024 < \theta < 0.105$**
for^2	0.000	0.001	$-0.002 < \theta < 0.002$	0.000	0.001	$-0.002 < \theta < 0.001$
disturb	-0.002	0.057	$-0.113 < \theta < 0.109$	-0.022	0.044	$-0.109 < \theta < 0.064$
wet	0.093	0.214	$-0.328 < \theta < 0.513$	0.083	0.166	$-0.244 < \theta < 0.409$
for × wet	0.033	0.019	$-0.005 < \theta < 0.071$	0.029	0.015	$-0.000 < \theta < 0.059$
GHOWocc	-0.298	0.554	$-1.383 < \theta < 0.787$	-0.307	0.438	$-1.165 < \theta < 0.552$
Barred Owl2008						
intercept (ψ)	2.004	1.345	$-0.633 < \theta < 4.641$			
for	0.227	0.119	$-0.006 < \theta < 0.460$	**0.042**	**0.014**	**$0.015 < \theta < 0.069$**
for^2	0.004	0.003	$-0.003 < \theta < 0.011$	**-0.001**	**0.001**	**$-0.003 < \theta < -0.000$**
disturb	0.028	0.089	$-0.146 < \theta < 0.202$	-0.025	0.042	$-0.108 < \theta < 0.058$
wet	-0.214	0.369	$-0.937 < \theta < 0.508$	-0.098	0.111	$-0.316 < \theta < 0.119$
for × wet	0.034	0.032	$-0.029 < \theta < 0.097$	0.015	0.009	$-0.002 < \theta < 0.032$
GHOWocc	-0.280	0.868	$-1.981 < \theta < 1.421$	-0.076	0.432	$-0.923 < \theta < 0.771$
Northern Saw-whet Owl 2007						
intercept (ψ)	2.782	1.640	$-0.432 < \theta < 5.995$			
for	0.044	0.047	$-0.048 < \theta < 0.136$	0.011	0.011	$-0.011 < \theta < 0.034$
for^2	-0.001	0.001	$-0.003 < \theta < 0.001$	0.000	0.000	$-0.001 < \theta < 0.000$
disturb	0.119	0.086	$-0.049 < \theta < 0.286$	0.029	0.032	$-0.034 < \theta < 0.093$
wet	1.826	1.161	$-0.450 < \theta < 4.102$	0.206	0.121	$-0.031 < \theta < 0.443$
for × wet	**0.074**	**0.031**	**$0.013 < \theta < 0.135$**	0.009	0.009	$-0.009 < \theta < 0.027$
GHOWocc	-1.042	0.823	$-2.656 < \theta < 0.572$	-0.184	0.404	$-0.975 < \theta < 0.607$
BDOWocc	0.302	0.887	$-1.436 < \theta < 2.040$	0.283	0.439	$-0.577 < \theta < 1.143$
Northern Saw-whet Owl 2008						
intercept (ψ)						
for				**0.045**	**0.020**	**$0.006 < \theta < 0.083$**
for^2				-0.002	0.001	$-0.003 < \theta < 0.000$
disturb				0.059	0.035	$-0.010 < \theta < 0.128$
wet				0.057	0.123	$-0.184 < \theta < 0.298$
for × wet				-0.018	0.012	$-0.040 < \theta < 0.005$
GHOWocc				0.109	0.515	$-0.901 < \theta < 1.119$
BDOWocc				-0.662	0.535	$-0.711 < \theta < 0.387$

Effects of covariates on occupancy

GHOW 2008

Great Horned Owl did not seem to be influenced by any landscape variables included in our models (Table 5). Accordingly, the model that only considered the detection covariates was ranked first according to the AIC_c values (Table 2).

BDOW 2007-2008

In 2007, Barred Owl was found in landscapes containing higher forest cover (Table 5). More specifically, a 1% increase in forest cover was associated with an 8.8% increase in the predicted odds of Barred Owl occupancy (Fig. 4). However, in 2008, none of the occurrence covariates contained in our models seemed to influence Barred Owl occupancy (Table 5). Although we predicted that the occurrence probability would decrease in presence of a Great Horned Owl or in disturbed forests, Barred Owl did not seem to be affected by these variables in our study. Finally, Barred Owl occurrence did not increase in wetlands and riparian habitats like we expected (Table 5).

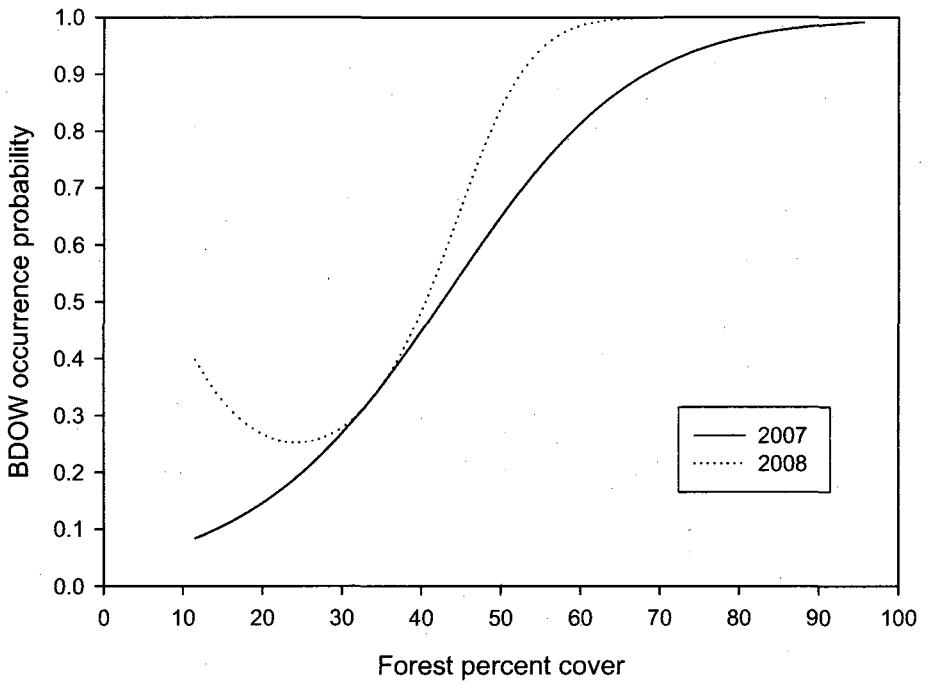

FIG. 4. Effect of forest cover within a 2-km radius on Barred Owl occupancy within agricultural landscapes of southern Québec, Canada. Predicted values were obtained following MacKenzie et al. (2002) and multi-model inference (see Table 5) under average conditions (Appendices 1 and 2) when using conspecific calls in an average landscape without predator or competitor. Note that 2008 is illustrated here to show constancy of results although forest cover did not significantly influence occupancy for that year.

NSWO 2007

Northern Saw-whet Owl occupancy showed a clear response threshold with respect to forest cover as it went from about zero to one when forest cover reached >30% (Table 5 and Fig. 5). Yet, the slope of this relationship was reduced in landscapes showing less than 10% cover in wetlands and riparian habitats (Table 5 and Fig. 5). Hence, contrarily to what was expected, the presence of wetlands and riparian habitats had a negative effect on Northern Saw-whet Owl occurrence. Similarly, neither the presence of predators or competitors in the landscape (GHOWocc and BDOWocc), nor the amount of disturbed forest cover seemed to decrease Northern Saw-whet Owl occupancy like we predicted (Table 5).

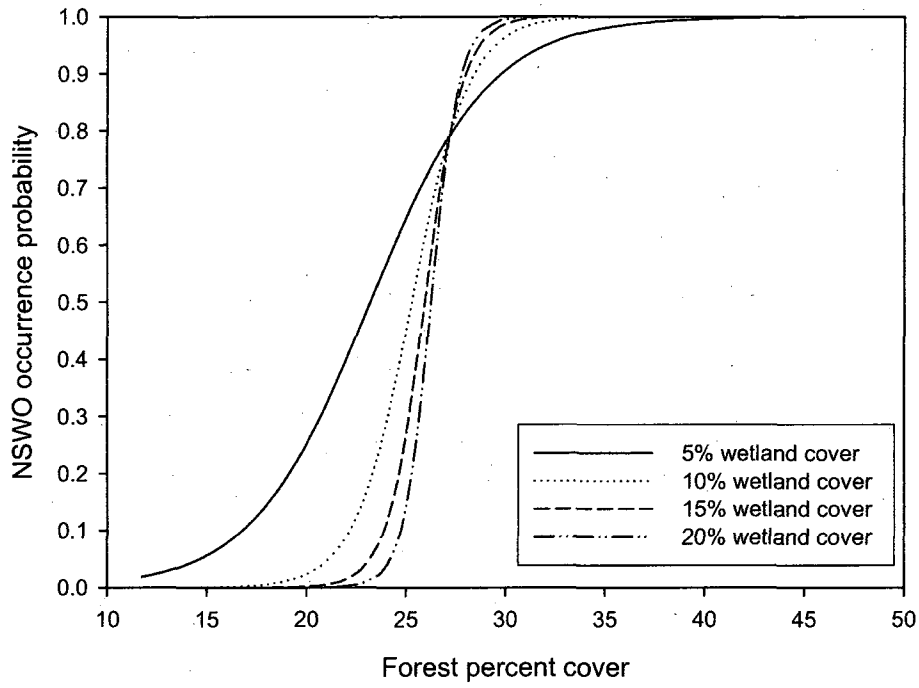

FIG. 5. Effect of forest cover within a 1km radius on Northern Saw-whet Owl occupancy for various wetland percent covers in 2007 within agricultural landscapes of southern Québec, Canada. Predicted values were obtained following MacKenzie et al. (2002) and multi-model inference (see Table 5) under average conditions (Appendices 1 and 2) when using conspecific calls in an average landscape without predator or competitor. Note that wetland cover includes both the water (rivers, lakes) riparian habitats and the actual wetlands (bogs, swamps, marshes).

Logistic regressions

According to logistic regressions, occurrence of Great Horned Owl was not affected by any landscape variable in either year (Table 5). Occurrence probability of Barred Owl increased with higher forest cover in both years (Table 5). While this increase was relatively linear in 2007, in 2008 Barred Owl occurrence probability showed a rapid increase with increasing forest cover followed by a plateau and ending with a slight decrease. Occurrence of Barred Owl did not seem to be influenced by any other variables (Table 5). Finally, although none of the variables affected the occupancy of Northern Saw-whet Owl in 2007, an increase in forest

cover was associated with an increase in Saw-whets' occurrence probability in 2008 (Table 5). Hence, results obtained using logistic regressions were different from those obtained through analyses that accounted for imperfect detection.

DISCUSSION

With this study, our main objectives were to quantify the influence of landscape structure and species interactions on the occurrence of owls. We also wanted to compare the detection probabilities in surveys using single-species broadcasts to those using multiple-species sequences including competitor or predator calls. Finally, we wanted to assess the importance of accounting for imperfect detection in owl surveys by comparing analyses that considered detection probability and others that did not.

Northern Saw-whet Owl was the species that occupied the highest proportion of sites in our study area, followed by Barred Owl and Great Horned Owl. Although the occurrence probability of Great Horned Owl did not appear to be affected by any landscape metrics, Barred and Northern Saw-whet Owl occupancy increased with forest cover. Moreover, the influence of forest cover on Northern Saw-whet Owl occupancy was less pronounced as the amount of wetlands and riparian habitats decreased in the landscape. Surprisingly, the presence of a predator or competitor did not seem to influence owl occupancy. While detection of Great Horned Owl seemed to be mostly influenced by the hour at which the survey was conducted, Barred and Northern Saw-whet Owl were affected by the type of broadcast used, time of year, and noise during the survey. Temperature also affected Northern Saw-whet Owl's detection probability. The low and variable detection probabilities obtained for all species stresses the importance of accounting for imperfect detection in owl surveys.

Detection

Broadcast

In our study, the probability of response to playbacks by Great Horned Owl was not affected by the type of broadcast used during the survey. Barred and Northern Saw-whet Owls were more responsive to conspecific than to heterospecific calls, concurrent with what was found by Bosakowski and Smith (1998). Although the calling activity of birds tends to increase when population density is high (McShea and Rappole 1997, Penteriani et al. 2002, Sexton et al. 2007), this did not seem to be the case for Barred Owl in this study. Detection of Barred Owl using conspecific playbacks was higher in 2007 even though the occurrence probability was lower compared with 2008. Great Horned and Barred Owls were previously found to be more responsive to playbacks of the smaller Northern Saw-whet Owl than to each other's heterospecific calls (Cannings 1993, Bosakowski and Smith 1998). Here, Bosakowski and Smith (1998) believed it was unlikely that the intent of the larger owls was to prey on the Saw-whets since they eagerly responded with hoots. However, our results did not show higher response of Great Horned and Barred Owls to Northern Saw-whet Owl calls. Furthermore, in three instances in our surveys, Barred Owls were observed approaching the source of the Saw-whet's broadcast without ever calling, leading us to think that predation might have been the goal of their moving closer.

Great Horned Owl playbacks affected Barred and Northern Saw-whet Owls to different extents. Barred Owls had a much higher detection probability when using the BDOW broadcast compared to when using the GHOW broadcast. However, the GHOW and GHOW+BDOW broadcasts had similar detection probabilities for Barred Owls. Hence, broadcasting Great Horned Owl playbacks before calling the Barred Owl had a strong negative impact on the latter's detectability. We thus suggest that the calling activities of Barred Owl might be inhibited by broadcasts of Great Horned Owl in an attempt to avoid harassment or predation. Yet, McGarigal and Fraser (1985) found that Barred Owls were not affected by playbacks of Great Horned Owls if the GHOW calls were broadcast after a 17-minutes BDOW survey. For their part, Northern Saw-whet Owls showed a much higher

detection probability when using the GHOW+NSWO broadcast compared to the GHOW broadcast. Here, although playbacks of Great Horned Owl did not inhibit the Saw-whet's calling activity *per se*, it did decrease its detection probability compared with the NSWO broadcast.

Overall, the negative impact of Great Horned Owl on detection probability was much stronger for Barred than for Northern Saw-whet Owls. Northern Saw-whet Owls are seasonal migrants (Cannings 1993, Marks and Doremus 2000) and must establish a new territory before breeding, whereas Barred Owls maintain their home range throughout the year (Mazur and James 2000, Johnsgard 2002). Hence, Northern Saw-whet Owls might be more inclined to respond to conspecific calls even after a predator was heard in order to secure their territories. On the other hand, Northern Saw-whet Owl's occurrence probability was estimated to be 0.94. Such a high occupancy level must have resulted in high densities, inciting the owls to increase their calling activities (McShea and Rappole 1997, Penteriani et al. 2002, Sexton et al. 2007). Yet, the low detection probability (0.23) we estimated, which makes it unlikely for owls to respond to playbacks, brings questioning on the strength of this hypothesis.

In order to avoid over-parameterization and convergence problems, we were constrained to keep simpler models and to discard variables that were less imperative to our analyses. Since Great Horned Owl playbacks had an impact on the detectability of the other species, it would have been interesting to determine whether the actual presence of Great Horned Owls in the landscape influenced Barred and Northern Saw-whet Owl calling activities. According to Crozier et al. (2006), Spotted Owls responded less frequently to conspecific calls following Barred Owl playbacks. Moreover, they found that Spotted Owls living in proximity to Barred Owls responded more to conspecific calls than unexposed individuals.

We would also have liked to consider the interaction between the different broadcast sequences and Julian date. Owls might have responded differently to broadcasts depending on the timing within the breeding season. Furthermore, the use of recorded calls generally seems to increase detection of many species after the broadcast (Mosher et al. 1990, Haug and

Didiuk 1993, Hardy and Morrison 2000, Takats et al. 2001). Yet, some species show higher detection rates when using passive auditory surveys, as Penteriani et al. (2002) observed for the Eagle Owl (*B. bubo*), which is the European counterpart of the Great Horned Owl (Johnsgard 2002). Since no control surveys were done in our study, it was not possible to determine whether the use of broadcasts increased the calling activity of owls compared with passive auditory surveys.

Date

Owl detectability varies between, and possibly throughout the seasons (Takats et al. 2001, MacKenzie 2005b). Some studies found that Great Horned Owls were mostly vocally active during the month of December through March (Johnsgard 2002). They seemed to be more vocal early in the breeding season (e.g., January) and to decrease their calling activity in mid-February in Wisconsin and Southern New Jersey (Morrell et al. 1991, Houston et al. 1998). Yet, we did not observe any variation in detection probability of Great Horned Owl for the total duration of our study (January-May). Barred Owls are usually heard through the months of February to April, with a peak in late March and April (Mazur and James 2000, Johnsgard 2002). Similarly, our results showed an increase in detection probability throughout the breeding season. This increase was more pronounced in 2007 compared with 2008 and did not follow the same pattern. In 2007, Barred Owl detection probability increased steadily throughout the season. However, it remained relatively low and stable for the first half of the 2008 season and increased rapidly for the second half. Thus, Barred Owls started to increase their calling activities later in 2008. Detection probability of Northern Saw-whet Owl was found to decrease throughout the duration of the breeding season in Wisconsin (Swengel and Swengel 1997). Our results concord with this observation. Given that Northern Saw-whet Owls are migrants (Cannings 1993, Marks and Doremus 2000), they have a limited time to reproduce and to raise their young before the fall migration in September-November (Cannings 1993). Hence, they may have to invest time and energy into their young rather than for calling once they secured a territory and a mate.

Hour

For many owls, calling activity was observed to be highest within the two-hour period following sunset and just before sunrise, and to be the lowest in the middle of the night (Ganey 1990, Takats and Holroyd 1997). However, our results did not show any such pattern for any species. In fact, detection probability of Barred and Northern Saw-whet Owl remained stable throughout the night (1- 9 hours after sunset), while Great Horned Owl detection increased during the same period (Fig. 3). Similarly, Morrell et al. (1991) observed that Great Horned Owl was more vocally active after midnight than before midnight (surveys: 16:00-08:00) in Pennsylvania. Currently, most owl monitoring programs ask volunteers to complete their survey routes before midnight (Takats et al. 2001, Balej 2006, Bird Studies Canada 2008). However, this restriction may be useless for Barred and Northern Saw-whet Owls, or even detrimental for detecting Great Horned Owl, at least in Southern Québec. Hence, owl survey schedules should be carefully planned to ensure they are conducted when owls are most vocally active.

Other factors

Some studies conducted in Alberta found that owls tend to decrease their calling activity in very cold weather (Takats and Holroyd 1997, Takats et al. 2001). However, Northern Saw-whet Owl was the only species that exhibited such a response to temperature in our study. Indeed, in spite of comparable temperatures, we did not observe a decrease in detection probability for Great Horned and Barred Owl when temperatures were cold. Background noise decreased Barred and Northern Saw-whet Owl detectability. Yet, we were surprised that Great Horned Owl detection was not affected by noise level even though all surveys were exposed to the same noise distractions. As should be expected in all sampling procedure relying on observer skills (Sauer et al. 1994), we found some variation in detection probability among observers. Finally, since Pacifici et al. (2008) found that detection probability was influenced by the type of forest, we thought landscape characteristics might also influence detection. However, having to discard some variables to keep simpler models, we chose not to include any landscape variables into the detection probability covariates.

Occupancy

GHOW

Great Horned Owl is a generalist species that is found in a large array of habitat types (Laidig and Dobkin 1995, Houston et al. 1998, Johnsgard 2002). This most probably explains why none of the landscape metrics seemed to influence occupancy of this species in our study. In fact, agricultural landscapes like those found in our study area should typically be attractive to Great Horned Owl since food is easily available in open spaces, while large tracts of forest and natural vegetation are also present for roosting and nesting (Houston et al. 1998, Johnsgard 2002). Moreover, Grossman et al. (2008) found an increase in Great Horned Owl occupancy in agricultural landscapes with intermediate levels of forest cover (36%-65%). This result may also suggest that Great Horned Owl may be able to adapt better to habitat change than other owl species.

BDOW and NSWO

Barred and Northern Saw-whet Owl both selected habitats with higher forest cover. Knowing that agriculture and forest cover were highly correlated (Fig. 2; 1-km radius: r = -0.92; 2-km radius: r = -0.91), we may conclude these species possibly avoided agriculture. Being habitat specialists depending on cavities for nesting (Cannings 1993, Postupalsky et al. 1997, Mazur and James 2000, Johnsgard 2002), these species rely on mature forests where old and large trees prone to cavity development are available. Grossman et al. (2008) observed in agricultural landscapes that Barred Owl was more likely to be found in habitats with >66% forest cover. These results are similar to those obtained here where the occurrence probability of Barred Owl surpassed 90% when forest cover was >68% (Fig. 4). However, even though the same trend was observed in 2008, forest cover did not significantly affect Barred Owl's occupancy in that year (Table 5). This difference may be explained by higher owl density in 2008 (Table 3). At higher density, some individuals might have to settle in less suitable habitats, masking their preference for high forest cover. This idea was also proposed by Riffell and Gutzwiller (2009) to explain interannual variation in bird-landscape relations, even though

their data did not support this hypothesis. Longitudinal studies are urgently required to better understand the causes of interannual variation in such bird-landscape relations.

Northern Saw-whet Owl occupancy showed a clear response threshold with respect to forest cover as it went from about zero to one when forest cover reached >30% (Fig. 5). Such a threshold was not detected by Grossman et al. (2008) who observed that over 90% of agricultural landscapes with >15% forest cover were occupied by Northern Saw-whet Owl in central Alberta. The lack of threshold in Grossman et al.'s study may originate from a lack of forest habitat specificity by the birds in their study, as a result of local adaptation to environmental disturbance (Both and te Marvelde 2007) or high population density (Riffell and Gutzwiller 2009). Yet, the presence of a threshold in Grossman et al.'s study could also have been masked from working at a greater spatial scale (15 km^2 in their study vs 3 km^2 in our study) and having considered a site occupied if a bird was detected in at least one of two consecutive years. Nevertheless, Hinam and St. Clair (2008) found that high levels of forest loss and fragmentation reduced the success and increased the physiological stress of breeding Northern Saw-whet Owls in the aspen parkland of central Alberta, thereby identifying potential mechanisms by which a threshold response to habitat loss and fragmentation may occur.

Barred and Northern Saw-whet Owl are often associated with the presence of wetlands and riparian habitats (Cannings 1993, Mazur et al. 1997, Mazur and James 2000, Hinam and Duncan 2002, Johnsgard 2002). Yet, these species did not seem to be associated with such habitats in this study (Table 5). In fact, the occurrence probability of Barred Owl was unaffected by the presence of wetlands and riparian habitats, whereas for a given level of forest cover, an increase in those habitat types decreased the occurrence probability of Northern Saw-whet Owl (Fig. 5). This discrepancy could possibly be explained by various non-mutually exclusive factors such as the availability and abundance of prey and nest sites in the wetland and riparian habitats, or by the occurrence of an important predator or competitor that would discourage the owls to settle there. Yet, such information are lacking for us to discriminate among those potential explanations.

Contrarily to what was predicted, disturbed forests did not decrease Barred and Northern Saw-whet Owl occupancy (Table 5). While Barred Owl is known to be negatively affected by disturbed forest (Haney 1997, Mazur and James 2000, Johnsgard 2002), Northern Saw-whet Owl's response to these habitats is not well documented. Nonetheless, regenerating forests do not seem to be suitable habitats for Saw-whet Owls (Cannings 1993). However, the impact of disturbed forest in an agricultural context might be less noticeable than in a forest-dominated one since disturbed-forest habitat quality contrasts much less sharply with that of undisturbed forest habitats than with respect to that of agricultural fields.

Considering that Great Horned Owl is a predator and competitor of the other two species (Cannings 1993, Houston et al. 1998, Mazur and James 2000, Johnsgard 2002), we predicted that the occurrence probability of Barred and Northern Saw-whet Owl would decrease in habitats where it is present. Similarly, we expected that Barred Owl would influence Northern Saw-whet Owl occupancy. Yet, we found that neither species was affected by the occurrence of a predator or competitor in the landscape (Table 5). In previous studies, Barred Owl was found to avoid Great Horned Owl in areas where woodlands were relatively small (Bosakowski and Smith 1998, Mazur and James 2000). On the other hand, in habitats where forest was more abundant, the two species were found to coexist while maintaining some sort of temporal segregation (McGarigal and Fraser 1985, Laidig ad Dobkin 1995, Mazur and James 2000). For their part, it was never clearly demonstrated that Northern Saw-whet Owl was influenced by the presence of the other two species. Yet, it was sometimes assumed that they would be avoiding Great Horned and Barred Owl. Nevertheless, Grossman et al. (2008) recently observed that Northern Saw-whet and Great Horned Owl were often found in the same landscapes, but they hypothesized that Saw-whets might have used different habitats to avoid Great Horned Owl. Again, model convergence problems prevented us to test for the presence of interactions between forest and Great Horned Owl occupancy, or between forest and Barred Owl occupancy in order to investigate whether the influence of forest cover depends on the presence of a predator or competitor.

In this study, the coexistence of Barred and Northern Saw-whet Owl with their predator or competitor may have resulted from high population densities. Indeed, occurrence probability was relatively high for the two species. Hence, they might not have been able to move away from the undesirable owls. Another possible explanation would be that some kind of segregation might take place in an agricultural context as the different species may not use the same habitats. For instance, Great Horned Owl may seek open habitats (e.g., agricultural fields) for foraging, while the other two species may keep away from open spaces. However, since Barred Owl was strongly affected by Great Horned Owl broadcasts, if previous studies would have accounted for imperfect detectability, they might have come to different conclusions. Barred and Great Horned Owl may not be spatially segregated but rather use other strategies (e.g., behavioral avoidance) to avoid agonistic encounters. As previously discussed, detectability of Northern Saw-whet Owl did not seem to be seriously affected by Great Horned Owl calls. Hence, the general idea that the smaller Saw-whet would be displaced by the larger Great Horned Owl may be unfounded as these two species may actually coexist in the wild.

Additional variables of interest

We would have liked to consider the influence of many more variables potentially affecting occupancy but, as mentioned earlier, we were constrained to keep simpler models to avoid over-parameterization and convergence problems. For instance, we would have liked to distinguish between the types of forest (i.e.: deciduous, mixed and coniferous) to better understand the habitat preferences of owl species. Two other landscape configuration variables had also been calculated: forest total core area (i.e., amount of forest left once 30 m of edge is removed) and total edge. We thought it would be interesting to assess the influence of the first variable since species negatively affected by habitat fragmentation (e.g., Barred Owl [Mazur and James 2000]) would tend to select patches with higher total core area. However, this variable was highly correlated with forest cover (r = 0.95 for both 1-km and 2-km radii) and we had to exclude it from our analyses. We were also interested in the influence of the amount of forest edge since it seems to influence owls' habitat selection (Mazur and James 2000, Grossman et al. 2008, Hinam and St. Clair 2008). Unfortunately, the relative area covered by

forest edges in our landscapes was too low (1-km radius: range = 0.07-0.30%; 2-km radius: range = 0.07-0.22%) to include this variable in the analyses.

Accounting for imperfect detection

Analyses that corrected for an imperfect detection (i.e., MacKenzie et al. 2002) and those that did not (i.e., logistic regression) resulted in slightly different conclusions (Table 5). Great Horned Owl was the only species that got identical results with both analyses, namely that its occurrence was not influenced by any landscape metrics. For Barred Owl, both types of analyses showed a positive effect of forest cover on occupancy in 2007, yet the magnitude of the effect seemed to be lower in logistic regressions (Table 5). Moreover, logistic regressions identified a quadratic effect of forest cover in 2008, while no landscape variables were found to affect occupancy when accounting for imperfect detectability. Finally, Northern Saw-whet Owl occupancy was affected by the interaction between wetlands and forest cover in 2007 when correcting for imperfect detectability. But when using logistic regressions for the same year, none of the landscape metrics seemed to influence this species. Hence, if detection probability had not been considered, Northern Saw-whet Owl might have appeared to be a generalist species in 2007, which it is not. Whether it changes the significant state of the different variables or the magnitude of the effect, detection probability really does have an impact on final results. Other studies that were conducted on small mammals and frogs have also shown that not accounting for detection probability yields bias in parameter estimation of logistic regression models (Gu and Swihart 2004, Mazerolle et al. 2005). As Gu and Swihart (2004) pointed out, these models are sensitive to even low levels of imperfect detection. Thus, accounting for detection probability reduces the chances of making erroneous inferences by bringing a new level of precision and accuracy to the analyses.

CONCLUSION

Several studies have described the influence of landscape on owl occupancy. Here, we have been able to compare landscape use by a generalist species (i.e., Great Horned Owl) and two specialist species (i.e., Barred and Northern Saw-whet Owl) in an agricultural context. While the generalist's occupancy was not influenced by landscape variables, the two specialists selected habitats with higher forest cover, and most possibly avoided agriculture. Hence, specialist species might be more vulnerable to habitat loss through agriculture intensification than generalist species. Yet, since Northern Saw-whet Owl only required >30% forest cover to reach occurrence probabilities that approached 1, they might be rather tolerant to habitat change. This study also failed to show that species interactions influence owl occupancy. However, broadcasting of Great Horned Owl calls did have an impact on owl detectability. Furthermore, owls tended to respond more to conspecific than heterospecific calls. Hence, in addition to prioritizing conspecific calls, owl monitoring programs using call-playback surveys should be concerned with the impacts of species interactions on owl detectability. Single-species surveys should be preferred to multiple-species surveys. If multiple-species surveys must be used, they should carefully be studied *a priori* to better understand how detection probability of the various species might be affected by the others. Most owl studies have neglected to account for imperfect detection even though many variables have been shown to influence owl detectability. Yet, our study shows that failing to do so may produce erroneous results.

ACKNOWLEDGEMENTS

We thank Benoit Gendreau and Marie-Claude Martin for their help in the field. Caroline Girard and Gabriel Diab provided precious assistance with geomatics. We are grateful to Marc Mazerolle for helping with the PRESENCE software. Thank you to Dany Garant and Marco Festa-Bianchet for their useful comments on this manuscript. We also thank Benoit Lapointe for his generous help with field logistics, and the graduate students of Marc Bélisle for their help in setting up the sites. Financial support for this project came from the Canada Research Chair in Spatial and Landscape Ecology, the Canadian Foundation for Innovation, the Fonds québécois de la recherche sur la nature et les technologies, the Natural Sciences and Engineering Research Council of Canada, and the Université de Sherbrooke.

APPENDIX 1. Average (± SD) conditions met during owl surveys conducted in agricultural landscapes of southern Québec, Canada.

	Great Horned and Barred Owl		Northern Saw-whet Owl	
	2007	2008	2007	2008
Date (Julian day) [A]	range: 32 to 150	range: 14 to 141	range: 1 to 103	range: 1 to 72
Time after sunset (hour)	4.42 ± 1.98 range: 1.00 to 9.00	4.44 ± 2.02 range: 1.00 to 8.98	4.35 ± 1.94 range: 1.00 to 9.00	4.19 ± 1.89 range: 1.02 to 8.68
Temperature (°C)	-1.7 ± 9.0 range: -25.0 to 19.2	-4.3 ± 8.8 range: -23.7 to 19.0	-0.1 ± 8.2 range: -25.0 to 19.2	0.9 ± 7.1 range: -20.2 to 19.0
Wind speed (km/h)	1.6 ± 2.3 range: 0.0 to 15.0	1.5 ± 1.7 range: 0.0 to 10.9	1.5 ± 2.0 range: 0.0 to 13.5	1.5 ± 1.7 range: 0.0 to 9.3
Noise level [B]	9.5 ± 6.1 range: 0 to 44	10.3 ± 5.9 range: 0 to 37	9.9 ± 6.1 range: 0 to 44	10.9 ± 5.9 range: 0 to 35

[A] For GHOW and BDOW, January 1st was considered to be Julian day 1. For NSWO, Julian day 1 corresponds to the first night the NSWO and GHOW+NSWO calling sequences were broadcast.
[B] See the Methods section for further information on the noise level variable.

APPENDIX 2. Average (± SD) land covers for the 112 sites surveyed for owls in southern Québec, Canada.

	r = 1 km	**r = 2 km**
Forest (%)	51.7 ± 21.2 range: 11.1 to 94.9	51.6 ± 17.3 range: 16.3 to 90.8
Disturbed forest (%)	5.6 ± 6.9 range: 0.0 to 33.1	5.5 ± 5.5 range: 0.0 to 24.6
Wetland and riparian habitats (%)	1.5 ± 2.8 range: 0.0 to 21.9	1.7 ± 2.3 range: 0.0 to 14.9

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CONCLUSION GÉNÉRALE

Cette étude a permis de comparer les préférences d'habitats d'une espèce généraliste (i.e., Grand-duc d'Amérique [*Bubo virginianus*]) et de deux espèces spécialistes (i.e., Chouette rayée [*Strix varia*] et Petite Nyctale [*Aegolius acadicus*]) de Strigidés. Alors que l'occurrence du généraliste ne semble pas être affectée par la structure du paysage, les spécialistes ont montré une préférence pour les habitats ayant un couvert forestier élevé et, par le fait même, un évitement des milieux agricoles. Cette observation nous porte à croire que, chez les Strigidés forestiers, les spécialistes seraient plus sensibles à la perte d'habitat causée par l'intensification de l'agriculture que les généralistes. Cependant, la probabilité d'occurrence de la Petite Nyctale s'approchait de 100% dès que le couvert forestier dépassait 30% du paysage. Celle-ci serait donc plus tolérante que la Chouette rayée face à la perte d'habitat. Cela concorde avec l'idée que les espèces migratrices soient moins affectées par la perte d'habitat que les espèces résidentes (Bender et al., 1998).

Contrairement à nos prédictions appuyées par la littérature (Cannings, 1993; Mazur et al., 1997; Mazur et James, 2000; Hinam et Duncan, 2002; Johnsgard, 2002), la probabilité d'occurrence de la Chouette rayée et de la Petite Nyctale n'a pas été accrue par la présence de milieux humides dans le paysage, ni diminuée par la présence de forêts perturbées. En fait, la Petite Nyctale a même démontré la relation inverse avec les milieux humides. Toutefois, nous avions peu de détails quant à la nature exacte de ces deux classes d'habitats (ex. : essence d'arbres présents, disponibilité de proies, présence de prédateurs, etc.). Ainsi, une caractérisation approfondie de ces classes d'habitats nous permettrait de mieux comprendre les mécanismes derrières les relations observées. De plus, répéter cette étude sur un plus grand nombre d'années pourrait s'avérer utile afin d'identifier les sources des variations interannuelles observées pour certains paramètres chez la Chouette rayée (Riffell et Gutzwiller, 2009).

Cette étude n'a pas été en mesure de montré que les interactions interspécifiques peuvent influencer la distribution des espèces de Strigidés dans l'espace. En effet, l'occurrence des Strigidés ne semblait pas affectée par la présence d'un prédateur ou d'un compétiteur. Cependant, la probabilité d'occurrence de la Chouette rayée et de la Petite Nyctale était relativement élevée, laissant sous entendre une densité de population élevée. Dans de telles circonstances, il se peut que les individus aient été incapables d'éviter la proximité avec leurs prédateurs ou compétiteurs. Plus d'études tenant compte de la probabilité de détection seraient nécessaires dans des milieux où les densités de population sont moins élevées afin de déterminer si les interactions interspécifiques ont réellement un impact sur la distribution des Strigidés.

La comparaison de différentes séquences d'enregistrements pour la repasse de chant a permit de confirmer que la séquence utilisée avait bel et bien un impact sur la probabilité de détection des Strigidés. D'abord, il est préférable d'utiliser le chant de l'espèce d'intérêt plutôt que le chant d'une autre espèce lors du recensement. Ensuite, la diffusion de chants du Grand-duc d'Amérique semble diminuer fortement la probabilité de détection de la Chouette rayée et dans une moindre mesure, la détectabilité de la Petite Nyctale.

Ainsi, à défaut d'influencer la distribution des Strigidés, les interactions interspécifiques affectent tout de même la détectabilité de certaines espèces. Seul le Grand-duc d'Amérique ne semblait pas affecté par le type de séquence utilisée. Toutefois, avec les données recueillies au cours de cette étude, il nous est impossible de savoir si l'utilisation de la repasse de chant augmente la probabilité de détection de celui-ci par rapport à un point d'écoute passif. Étant donnée l'impact que la diffusion de son chant a sur la détectabilité de certaines espèces, s'il était démontré que la repasse de chant n'améliore pas la détection du Grand-duc, nous recommanderions l'abandon de la diffusion de son chant dans tous les recensements de rapaces nocturnes. Autrement, les recensements de Grand-duc d'Amérique devraient être distincts de ceux des autres espèces afin d'éviter d'affecter leurs probabilités de détection.

Cette étude a permit de montrer l'impact du chant du Grand-duc d'Amérique sur la détectabilité de deux espèces de Strigidés. Toutefois, il faudrait faire de même à chaque fois qu'une séquence contenant plus d'une espèce est utilisée pour un recensement. Les interactions interspécifiques sont complexes et leurs effets sur la détectabilité des Strigidés sont encore mal connus.

Nous sommes conscients que certains éléments de notre méthode auraient pu être mieux standardisés. Par exemple, lors de la création de nos bandes sonores, nous aurions pu exclure le chant de la femelle Grand-duc d'Amérique et nous limiter aux enregistrements des chants territoriaux des mâles de chaque espèce. Nous aurions également pu ajuster la portée de ces enregistrements afin qu'elle soit identique pour chacune des espèces. Finalement, l'utilisation d'un appareil capable de mesurer l'intensité des bruits ambiants lors des recensements aurait apporté plus de précision. Cependant, nous croyons que les méthodes utilisées dans cette étude étaient semblables à celles qui sont couramment utilisées dans les recensements de rapaces nocturnes. Nous croyons donc que ces éléments n'ont pas apporté de biais supplémentaires par rapports aux recensements typiques.

Finalement, les résultats d'analyses qui ne tiennent pas compte de la probabilité de détection (e.g., régressions logistiques) étaient différents de ceux d'analyses qui corrigent pour une détection imparfaite (e.g., MacKenzie et al., 2002). Cette différence, ainsi que les faibles probabilités de détection moyennes obtenues pour chacune des espèces appellent à la prudence. En effet, une étude qui omet de considérer la probabilité de détection des Strigidés pourrait mener à des conclusions erronées. Il est donc absolument essentiel de tenir compte de la probabilité de détection lors de recensements de Strigidés.

Actuellement, aucun programme pour le suivi des rapaces nocturnes ne tient compte de la probabilité de détection. Certains changements s'imposent donc afin d'améliorer la qualité et la précision de ceux-ci.

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